

**Documentation for the Energy Modeling
and Analysis eXercise (EMAX)**

**Jason S. Link, Carolyn A. Griswold,
Elizabeth T. Methratta, and Jessie Gunnard, Editors**

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Documentation for the Energy Modeling and Analysis eXercise (EMAX)

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Abstract

The Northeast U.S. (NEUS) Continental Shelf Ecosystem is a dynamic environment. In order to evaluate the response of this ecosystem to numerous human-induced perturbations and to explore possible future scenarios, the Northeast Fisheries Science Center (NEFSC) instituted the Energy Modeling and Analysis eXercise (EMAX). The primary goal of EMAX was to establish an ecological network model (i.e., a nuanced energy budget) of the entire NEUS Ecosystem food web. The highly interdisciplinary EMAX work focused on four contemporary (1996-2000) subregions of the ecosystem; designated 36 network nodes (biomass state variables) across a broad range of the biological hierarchy; and incorporated a wide range of key rate processes. The emphasis of EMAX was to explore the particular role of small pelagic fishes in the ecosystem, and various model configurations were constructed and pseudo-dynamic scenarios evaluated to explore how potential changes to this group can affect the rest of the food web. Preliminary results show that small pelagic fishes are clearly keystone species in the ecosystem. There are some differences across the four EMAX regions reflective of the local biology, but major patterns of network properties are similar over space. EMAX will continue to play a critical role in the further development of an ecosystem approach to fisheries (EAF) by acting as a catalogue of information and data; identifying major fluxes among biotic components of the ecosystem; serving as a basis for further analytical models; developing a way to evaluate biomass tradeoffs; and acting as a backdrop for a suite of other relevant management and research questions.

Preface

This document serves to capture the methodologies we used in the Energy Modeling and Analysis eXercise (EMAX) to present the parameter values across all taxa (biomass, consumption, production, respiration, other rate estimates, diet compositions, etc.). The intent is not to provide particular scenarios or detailed analyses of the networks modeled, nor to present results of any particular group, as many of these are reported in other venues. Rather, we wanted to document the methodological approaches we used in one place for future reference.

Each subject matter expert or group of experts is noted as the lead for each section, and references are kept within each section for proximity to the subject matter.

The document is organized into four main sections. First is an introduction which provides the background context and rationale for why we undertook this exercise. A list of acronyms is provided here.

The second and largest section is a series of chapters outlining how biomasses were estimated for each of the network nodes. The format of each generally follows the same outline. First, any relevant background information is provided, including a species list. Next is an annotation (with references) of the data sources from which biomass estimates were obtained. Following that is a section noting the quantitative approaches for estimation, and finally, any germane example results are presented to help clarify the methodology. We also include the major rate values where appropriate.

The third section treats respiration, consumption, diet composition, fisheries and other removals separately. These parameters are common across nodes and as such are presented distinct from any particular node. This section also includes the modeling protocols and how we constructed, balanced, and utilized the network.

Finally there is a discussion section which includes a glossary and appendix of the input matrices. The discussion reports on key data gaps and lessons learned from EMAX; the glossary defines some key terms used in the model; and the appendix presents the prebalanced data matrices.

Nearly twenty researchers worked to bring information together for this reference document, and we hope it will well serve future EMAX efforts.

Jason S. Link, Ph.D.
EMAX Chair

List of Acronyms

AVHRR	Advanced Very High Resolution Radiometer
AE	assimilation efficiency
BCD	bacterial carbon demand
BENCAT	Benthic Survey Catch (Database)
BGE	bacterial growth efficiency
BTS	bottom trawl survey
BW	body weight
CETAP	Cetacean and Turtle Assessment Program
CFDBS	Commercial Fisheries Database System
CV	coefficient of variation
DOC	dissolved organic carbon
DW	dry weight
EAF	ecosystem approach to fisheries
EBFM	ecosystem-based fisheries management
EE	ecotrophic efficiency
EMAX	Energy Modeling and Analysis eXercise
ERSEM	European Regional Seas Ecosystem Model
ESSG	Ecosystem Status Steering Group
ESWG	Ecosystem Status Working Group
FEP	Fisheries Ecosystem Plan
GARM	Groundfish Assessment Review Meeting
GB	Georges Bank
GGE	gross growth efficiency
GOM	Gulf of Maine
GUI	graphical user interface
HNLC	high nitrogen, low chlorophyll
IBP	International Biological Program
ICCAT	International Commission for the Conservation of Atlantic Tunas
MAB	Mid-Atlantic Bight
MARMAP	Marine Resources Monitoring Assessment and Prediction Program
MCMC	Monte Carlo Markov Chain
MCSST	Multi-Channel Sea Surface Temperature
MRFSS	Marine Recreational Fisheries Statistics Survey
LMR	Living Marine Resource
NABE	North Atlantic Bloom Experiment
NEFSC	Northeast Fisheries Science Center
NEPA	National Environmental Policy Act
NEUS	Northeast United States
NTS	non-target species
PAR	photosynthetically active radiation
PER	percent extracellular release
PETS	Protected, Endangered and Threatened Species
POC	particulate organic carbon
PS	protected species
SAW	Stock Assessment Workshop
SeaWiFS	Sea-viewing Wide Field-of-view Sensor
SNE	Southern New England
SST	sea surface temperature
TS	target species
US EEZ	United States Exclusive Economic Zone
VGPM	Vertically Generalized Productivity Model
VPA	virtual population analysis
WW	wet weight

1. Introduction

Why Do EMAX?

The Northeast U.S. (NEUS) Continental Shelf Ecosystem is a dynamic environment. The general observation is that it has shifted from a vertical to a horizontal system due to the resurgence of small pelagic fishes, namely herring and mackerel. With regard to this resurgence, the question is: How important have these small pelagics become to the success of other commercial fish stocks; protected, endangered and threatened species (PETS); National Environmental Policy Act (NEPA) species; and the overall functioning of the ecosystem? This issue has become increasingly important as multiple stakeholders have begun exploring potential tradeoffs in the NEUS Ecosystem.

More broadly, there have been numerous recent calls to adopt an ecosystem approach to fisheries (EAF, or Ecosystem-based Fisheries Management [EBFM]. Here EAF and EBFM are used synonymously). There are many rationales for why EAF is an emerging approach, such as competing stake-holders and legislation; debate over the importance of different processes (fishing, environment, predation, etc.); the need for explicit consideration of non-targeted species, protected species, habitats, etc.; and the need to directly assess tradeoffs among and within sectors and across biomass allocation. Central to these considerations is taking a more holistic look at an ecosystem and simultaneously evaluating tradeoffs among component biomass or user sectors.

To evaluate the response of this ecosystem to numerous human-induced perturbations and to explore possible future scenarios, the Northeast Fisheries Science Center (NEFSC) instituted the Energy Modeling and Analysis eXercise (EMAX). The primary goal of EMAX was to establish an ecological network model (i.e., a nuanced energy budget) of the entire NEUS Ecosystem food web.

The highly interdisciplinary EMAX work focused on four subregions of the ecosystem from contemporary times (1996-2000), had 36 network nodes (biomass state variables) across a broad range of the biological hierarchy, and incorporated a wide range of key rate processes. The emphasis of EMAX was to explore the particular role of small pelagic fishes in the ecosystem. Various model configurations were constructed and psuedo-dynamic scenarios were evaluated to explore how potential changes to the small pelagic fishes can affect the rest of the food web.

Why Do an Energy Budget and Network Analysis?

There are a wide range of approaches one could take to answer the question about the role of small pelagics. One way to explore holistic ecosystem perspectives and examine biomass tradeoffs is to use ecosystem models. Within the wide variety of possible ecosystem models, energy budgets and network analyses provide useful tools to evaluate relative biomass, system properties, and fluxes within an ecosystem. Many of these models allow one to explore the fate and flux of production within a system by explicitly tracking how the energy flows among various components of the system. Of the many network models available, we chose to use EcoPath and EcoNetwrk to evaluate various spatial, temporal, and hypothetical scenarios.

Key to our selection of a network analysis was the need to evaluate multiple processes and factors simultaneously and holistically. Further, the relative importance of any particular

process or biological group is hard to capture without a broader context of energy flows and standing stock biomass in an ecosystem. Additionally, we wanted to compile information as a catalogue for future endeavors, and constructing an energy budget for the entire ecosystem was an excellent way to integrate such information. There are many other rationales for doing an energy budget and network analysis, but the major consideration we kept returning to was that evaluating scenarios and tradeoffs cannot correctly be done in a vacuum. A broader context of ecosystem structure and dynamics is truly required to evaluate the issue of tradeoffs among component biomass or user sectors.

Background of the Working Group

The core of our Working Group (hereafter, WG) started out in mid-1998 as a reading group for interested staff at the Northeast Fisheries Science Center who wanted to keep abreast of current issues in fisheries science and management. After reading and discussing material on the subject (including Steve Hall's 1999 book) the WG realized it could make a positive contribution toward the implementation of EBFM. Since the NEFSC has some of the world's premier time series of fisheries-independent data on subjects such as fish, mammal, and bivalve species abundance, zooplankton biomass, and food habits and temperature, the WG thought it would be useful to assemble these data and document the current status and recent history of the NEUS Ecosystem.

The WG became the Ecosystem Status Working Group (ESWG) from 2000-2002 and produced a report on the status of the NEUS Ecosystem (Link and Brodziak 2002). The WG had a vast array of personnel from a wide range of disciplines covering physics, biology, and social sciences. As 2002 ended, the core of the WG recognized a need to do more than simply compile a catalog of information. Several factors external to the NEFSC were influencing the prominence of ecosystem considerations and were expected to continue. Such factors included a global increase in calls for ecosystem-based approaches to fisheries management; potential changes to key U.S. legislation; two high-level Commission reports on the world's oceans; continuing conflicts across living marine resource (LMR) user sectors; important initiatives within NOAA and NMFS; and a regional recognition of LMR management complexity.

The ESWG morphed into the Ecosystem Status Steering Group (ESSG), which proposed multiple options for helping the NEFSC deal with these external considerations of mutual interest to the NEFSC's priorities, stakeholders, and the members of the WG itself. The ESSG set out to identify and develop a project that would form the basis for a fishery ecosystem plan. In developing EMAX, the ESSG decided it required:

- Broad Center involvement
- An interdisciplinary perspective
- A high degree of management relevancy
- The ability to serve as a pilot project, meaning that it would be short term in nature but designed with long term perspective in mind
- Be in the context of ultimately supporting a fisheries ecosystem plan (FEP)

After discussions with senior NEFSC staff during 2002-2003, an internal proposal was accepted and there began more formal analysis and examination of the region's ecosystems as a whole.

A network analysis-energy budget approach was determined a logical place to start for the construction and piecing together of relevant, interdisciplinary data across the NEFSC's programs. It was recognized that after the assembly of a network, multiple questions could be addressed, but it was difficult to address questions beforehand. Thus, in late 2003 the Energy Modeling and Analysis eXercise (EMAX) was formed from the core WG.

Emphasis of EMAX

The following outlines our original question and terms of reference. Some of the major products and deliverables proposed for this project are also listed.

Specific Question

What is the role of small pelagic fish in the NEUS Ecosystem as determined by a recent network analysis?

Why emphasize small pelagics as a pilot project? These organisms are keystone species, are found at mid trophic levels, interact with a large number of other species, are currently highly abundant, and have a minimal fisheries prosecuted on them (i.e., it was a relatively non-controversial issue).

Terms of Reference

1. For the NEUS Ecosystem, what are the annual, seasonally-resolved values for the following for each of the major sub-ecosystem regions over the past 5 years or so (1996 – 2000)?
 - A. Primary production
 - B. Secondary production (both zooplankton and benthos, as data permits)
 - C. Fish production
 - D. Marine mammal and bird production
 - E. Fishery production (in terms of catch, landings, etc.)
2. What is the transfer efficiency between trophic levels or black boxes (i.e., develop an integrated and balanced energy budget)?
3. What is the role of small pelagics relative to other species in the ecosystem?

Proposed Key Deliverables

- Understanding the relative role of small pelagic species simultaneously with other organisms (target species [TS], non-target species [NTS], and protected species [PS])
- Examining how changes to small pelagics could potentially affect management of these and other interacting species
- A compiled set of integrated information and data
- Basis for further FEP efforts
- Basis for further modeling
- Identification of information gaps

Spatial and Temporal Extent

Our analyses cover 1996 to 2000. The choice was made to produce annualized estimates integrated across the appropriate seasonality for each taxa group. We separated the NEUS Ecosystem into four main subregions (ecoregions): Gulf of Maine (GOM), Georges Bank (GB), Southern New England (SNE), and Mid-Atlantic Bight (MAB) (Figure 1.1). These principally correspond to the major regions of the Center's bottom trawl survey (BTS; Table 1.1) according to a commonly-defined strata set, but also account for key oceanographic, sediment, and bathymetric considerations.

Network Nodes

In network parlance, a node is analogous to a box, group, etc., and this usage was adopted for EMAX. The current network configuration has 36 nodes, representing a wide amalgamation of species (Table 1.2). Each node can potentially interact with other nodes, and the network configuration is shown in Figure 1.2. Each node was not necessarily represented in each ecoregion (e.g., there are no pinnipeds on Georges Bank), but the vast majority were. A glossary of terms (see Section 26) provides further information about common network and energy budget concepts.

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- Hall, S.J. 1999. *The effects of fishing on marine ecosystems and communities*. Oxford, UK: Blackwell Publishing Ltd; 274 p.
- Link, J; Brodziak, J, eds. 2002. Report on the Status of the NE US Continental Shelf Ecosystem. NEFSC Ecosystem Status Working Group. *Northeast Fish. Sci. Cent. Ref. Doc.* 02-11; 245 p.

Table 1.1. NEFSC Bottom Trawl Survey Strata used to define the four main EMAX regions.

Survey stratum definitions	Strata		Area (square kilometers)
	Inshore	Offshore	
Gulf of Maine (GOM)	57-90	24, 26-30, 36-40	79127.95
Georges Bank (GB)	NA	13-23, 25	43666.16
Southern New England (SNE)	1-14, 45-56	1-12	64060.37
Mid-Atlantic Bight (MAB)	15-44	61-76	59807.29

Table 1.2. EMAX network nodes and numbers.

Node Name	Node #
Phytoplankton - Primary Producers	1
Bacteria	2
Microzooplankton	3
Small Copepods	4
Large Copepods	5
Gelatinous Zooplankton	6
Micronekton	7
Mesopelagics	8
Macrobenthos - Polychaetes	9
Macrobenthos - Crustaceans	10
Macrobenthos - Molluscs	11
Macrobenthos - Other	12
Megabenthos - Filterers	13
Megabenthos - Other	14
Shrimp and Similar Species	15
Larval Fish - All	16
Small Pelagics - Commercial	17
Small Pelagics - Other	18
Small Pelagics - Squid	19
Small Pelagics - Anadromous	20
Medium Pelagics - (piscivores and other)	21
Demersals - Benthivores	22
Demersals - Omnivores	23
Demersals - Piscivores	24
Sharks - Coastal	25
Sharks - Pelagics	26
Highly Migratory Species - (tuna, billfish and swordfish)	27
Pinnipeds	28
Baleen Whales	29
Odontocetes	30
Sea Birds	31
Fisheries - Demersal	32
Fisheries - Pelagic	33
Discards	34
Detritus - POC	35
DOC	36

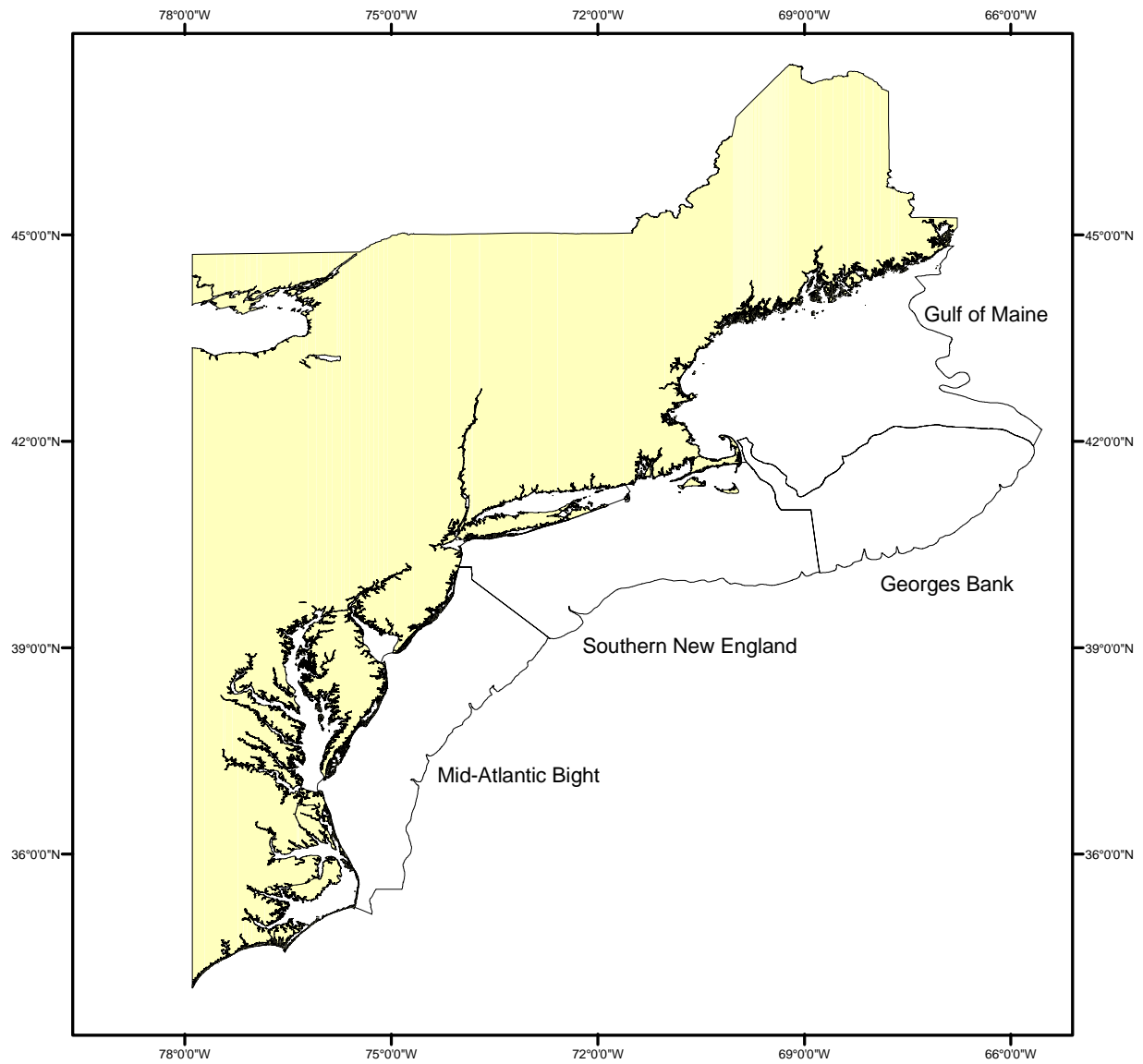


Figure 1.1. Map of the Northeast U.S. Continental Shelf Ecosystem and its four major subregions.

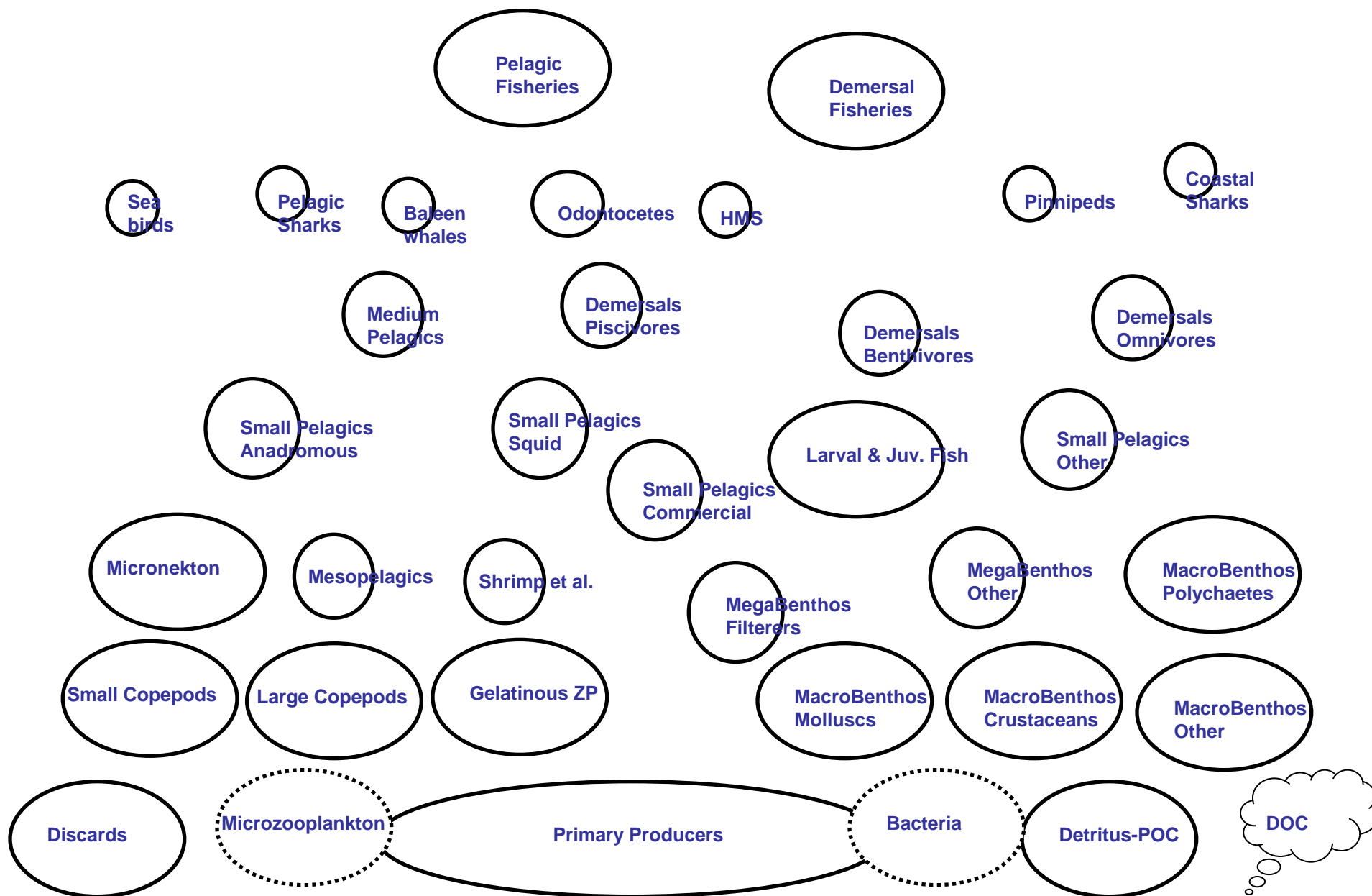


Figure 1.2. Major nodes of the EMAX network.

2. Phytoplankton and Primary Production

John E. O'Reilly and David D. Dow (node #1)

Background/Data Sources

Biomass

The broad-scale patterns in the spatial and seasonal distribution of phytoplankton biomass in the NEUS Ecosystem were described by O'Reilly and Zetlin (1998). These patterns were derived from 57,088 measurements of chlorophyll *a* made during 78 NEFSC MARMAP (Marine Resources Monitoring, Assessment, and Prediction Program) surveys conducted between 1977 and 1988. Additionally, we have developed a comprehensive time series of surface chlorophyll concentration for the NEUS based on SeaWiFS (Sea-viewing Wide Field-of-view Sensor) ocean color data collected since September 1997.

Production

Phytoplankton primary productivity measurements (^{14}C uptake rate) made during MARMAP surveys between 1977 and 1982 revealed that the Northeast shelf is among the most productive shelf ecosystems in the world (O'Reilly *et al.* 1987). While the *in situ* ^{14}C uptake method provides precise estimate of primary productivity, this method is expensive and labor-intensive, and therefore it is difficult to obtain sufficient spatial and temporal coverage to assess annual variability and long-term trends. At present, combining remotely-sensed data from satellites with productivity algorithms (Campbell *et al.* 2002) represents the only feasible method for resolving seasonal, annual, and climate-related variability of primary productivity throughout large marine ecosystems.

Quantitative Approach for Biomass Estimates

Estimates of standing stocks of phytoplankton biomass in the water column were based on chlorophyll *a* (Chl) concentrations and two approaches. The first approach used MARMAP vertical profiles of chlorophyll *a* pigment which were vertically integrated over the water column to a depth of 75 m (or bottom if $< 75\text{m}$) to yield mg Chl m^{-2} . Vertically-integrated chlorophyll (mg Chl m^{-2}) was averaged by standard stations/tiles (O'Reilly and Zetlin 1998) and by six bimonthly seasons. The annual mean (mg Chl m^{-2}) was computed for each station/tile from the six seasonal means. The annual means for each station/tile were then weighted by the area of each tile to generate the average phytoplankton standing stock (mg Chl m^{-2}) for the GOM (Gulf of Maine), SNE (Southern New England), GB (Georges Bank), and MAB (Mid-Atlantic Bight) regions.

The second approach used remotely sensed estimates of near surface Chl from 1,450 high-resolution SeaWiFS scenes of the region and the vertical profile model of Morel and Berthon (1989) to derive mg Chl m^{-2} for the euphotic layer from surface estimates. For these analyses, satellite data were processed according to the methods of Fu *et al.* (1998) and were mapped using a standard projection with an image size of 1024×1024 pixels and a resolution of $1.25 \times 1.25 \text{ km}$ per pixel. Annual mean integral chlorophyll (mg Chl m^{-2}) values for each pixel

were constructed from monthly means, and these were averaged to yield regional estimates of phytoplankton standing stocks (mg Chl m^{-2}).

Biomass Results

Table 2.1 compares estimates of phytoplankton biomass made by vertically integrating *in situ* data from MARMAP surveys with those based on SeaWiFS satellite estimates in Table 2.1. Since the SeaWiFS/Morel and Berthon Model estimates represent integral stocks in the euphotic layer and the MARMAP estimates are integrated standing stocks in the upper 75 m of the water column, we expect the latter estimates to be greater than the former. The MARMAP estimates are slightly higher than the satellite model-based estimates in the GOM but significantly higher in the other three regions.

Quantitative Approach for Estimates of Production

The Vertically Generalized Productivity Model (VGPM, Behrenfeld and Falkowski 1997) was used to estimate primary production. The VGPM incorporates remotely-sensed estimates of surface chlorophyll concentration and photosynthetically active radiation (PAR) from SeaWiFS and sea surface temperature (SST) from the NOAA AVHRR sensor (Advanced Very High Resolution Radiometer). In the VGPM, the optimal rate of productivity ($P_{b_{\text{opt}}}$: optimal water column carbon fixation [$\text{mg C } \{\text{mg chlorophyll } a\}^{-1} \text{ h}^{-1}$]) is modeled as a 7th order polynomial function of SST. In our application of the VGPM, which we designate VGPM2, the relationship between $P_{b_{\text{opt}}}$ and SST follows the exponential relationship by Eppley (1972), as modified by Antoine *et al.* (1996). A trial of the VGPM, VGPM2 and three other productivity models revealed that the VGPM2 yielded the best agreement with the MARMAP seasonal productivity cycle for the NEUS Ecosystem (O'Reilly and Ducas 2004) (Figure 2.1).

Daily VGPM2 estimates of primary production were computed for the 1998-2000 period using chlorophyll and PAR data from 1,450 high-resolution SeaWiFS scenes and SST data from 3,743 high-resolution nighttime AVHRR scenes of the Northeast U.S. SeaWiFS chlorophyll and PAR data were processed with SEADAS (Fu *et al.* 1998) and AVHRR SST was processed by NOAA CoastWatch using the MCSST algorithms (Multi-Channel Sea Surface Temperature). Satellite data were mapped using a standard projection with an image size of 1024 x 1024 pixels and a resolution of 1.25 x 1.25 km per pixel.

Phytoplankton Production Results

The generalized annual cycles of phytoplankton primary production for the four regions of the NEUS Ecosystem are illustrated in Figure 2.2. The annual mean primary production for each region is provided in Table 2.2.

Inputs to network models are usually in the form of organic carbon, calories, nitrogen, phosphorus, or wet weight. For this exercise, inputs to the network models were standardized to wet weight. Conversion of phytoplankton biomass and primary production from chlorophyll and carbon, respectively, to wet weight used factors provided in Table 2.3. The resulting GOM phytoplankton biomass value used in EMAX was $20.11 \text{ g wet wt m}^{-2}$. The net production value used in EMAX for the GOM was $3281.5 \text{ g wet wt m}^{-2} \text{ yr}^{-1}$, while the gross production was $4101.9 \text{ g wet wt m}^{-2} \text{ yr}^{-1}$. These wet weight estimates are derived assuming that organic carbon is

50% of the dry weight and the dry weight is 20% of the wet weight for phytoplankton, resulting in an overall conversion factor of 10 mg wet weight:mg carbon (Table 2.3). This is less than the 32.26 mg wet weight:mg carbon value used by Heymans (2001) (who assumed 3.23 mg dry weight:mg C and 10:1 wet weight:dry weight) for input to their model. Other studies employing the Ecopath model, such as that of Dalsgaard and Pauly (1997), used a conversion factor of 10 mg wet weight:mg carbon, within the range for algal weight:carbon indicated by Strickland (1966) in Table 2.3.

It should be noted that there is some confusion in the literature regarding the appropriate conversion factor to convert phytoplankton organic carbon to wet weight. It is worthwhile to quote Strickland's distinction between algal weight and wet weight (1966, p.15):

Two "wet weights" must be recognized, the true wet weight of the cells themselves with no extraneous water and the experimental wet weight obtained after draining the cells in some standard manner. The first weight is obtained from algal cell volumes, as measured microscopically, and a specific gravity value which, for all practical purposes, may be taken as unity. To avoid confusion this quantity should be called, simply, algal weight. The experimental "wet weight" will vary considerably according to the technique employed and will rarely, if ever, be less than twice the true algal weight, due to the presence of interstitial water. The confusion of these two weight figures by some authors has caused serious errors when computing, for example, chlorophyll:carbon ratios from cell volumes.

From the foregoing, it appears that the 10-12 mg algal weight:mg C is the most suitable factor for estimating phytoplankton biomass as "wet weight".

The EcoNetwrk software requires estimates of gross production. Conversion of primary production values for input to EMAX assumes that our estimates of primary production based on the VGPM2 and ¹⁴C methods represent net primary production and that net primary production and phytoplankton respiration are respectively 80% and 20% of gross primary production. Marra and Barber (2004) estimated daily plankton respiration as twice the dark uptake of carbon-14, where the dark uptake averaged 20-25% of the uptake during the light. Gross primary production can be calculated directly using the oxygen change method over a 24 hour period with light and dark bottles. Marra and Barber (2004) found good correlation between their carbon-14 estimate of phytoplankton respiration and the respiration from the oxygen change method during the North Atlantic Bloom Experiment (NABE). During this experiment the heterotrophic and phytoplankton respiration contributed equally to the total water column respiration. For comparison, Duarte and Cebrian (1996) estimate that phytoplankton respiration is 35% of gross primary production.

We assumed that the percent extracellular release (PER) of dissolved organic carbon by phytoplankton is 15% of the net primary production, based on ¹⁴C-uptake results from O'Reilly *et al.* 1987 (Table 2.3). For comparison, Nagata (2000) reported PER values ranging from 5%-30% and an average value of 11.3% for samples from the Gulf of Maine.

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Table 2.1. Integrated water column chlorophyll *a* concentration (Chl mg m⁻²) for the Mid-Atlantic Bight (MAB), Southern New England (SNE), Georges Bank (GB) and Gulf of Maine (GOM) regions of the Northeast U.S. Continental Shelf Ecosystem. (MARMAP data represent the vertically integrated chlorophyll to 75 m or bottom if less than 75 m; SeaWiFS - Morel and Berthelon estimates represent integrated chlorophyll over the euphotic layer.)

Region	MARMAP 1977-1987	SeaWiFS - Morel and Berthelon Model 1998-2000
MAB	61.80	50.11
SNE	71.34	51.18
GB	77.36	49.43
GOM	52.73	50.29

Table 2.2. Mean phytoplankton primary production (g C m⁻² d⁻¹) based on the SeaWiFS data and the VGPM2 model.

Region	Primary Production 1998-2000
MAB	1.165
SNE	1.026
GB	0.900
GOM	0.900

Table 2.3. Phytoplankton conversions/comparisons.

Quantity	EMAX	Reported Values	Reference
mg C:mg Chl	40	30 30 30	Strickland 1966 Epply 1968 Banse 1977
mg dw:mg C	2	2	Strickland 1966
mg algal weight:mg dw	5	5	Strickland 1966
mg wet weight:mg C	10	32.26 10 16 10	Heymans 2001 Dalsgaard & Pauly 1997 Walsh 1981 Bundy 2004
mg algal weight:mg C		6.7-11.1	Strickland 1966
mg wet weight:mg Chl	400	500	Strickland 1966
Respiration:Gross PP	0.20	0.354 0.17-0.3	Duarte & Cebrian 1996 Cloern <i>et al.</i> 1995
Net PP:Gross PP	0.80		
Percent Extracellular Release	15%	15% 11.3%	O'Reilly <i>et al.</i> 1987 Nagata 2000

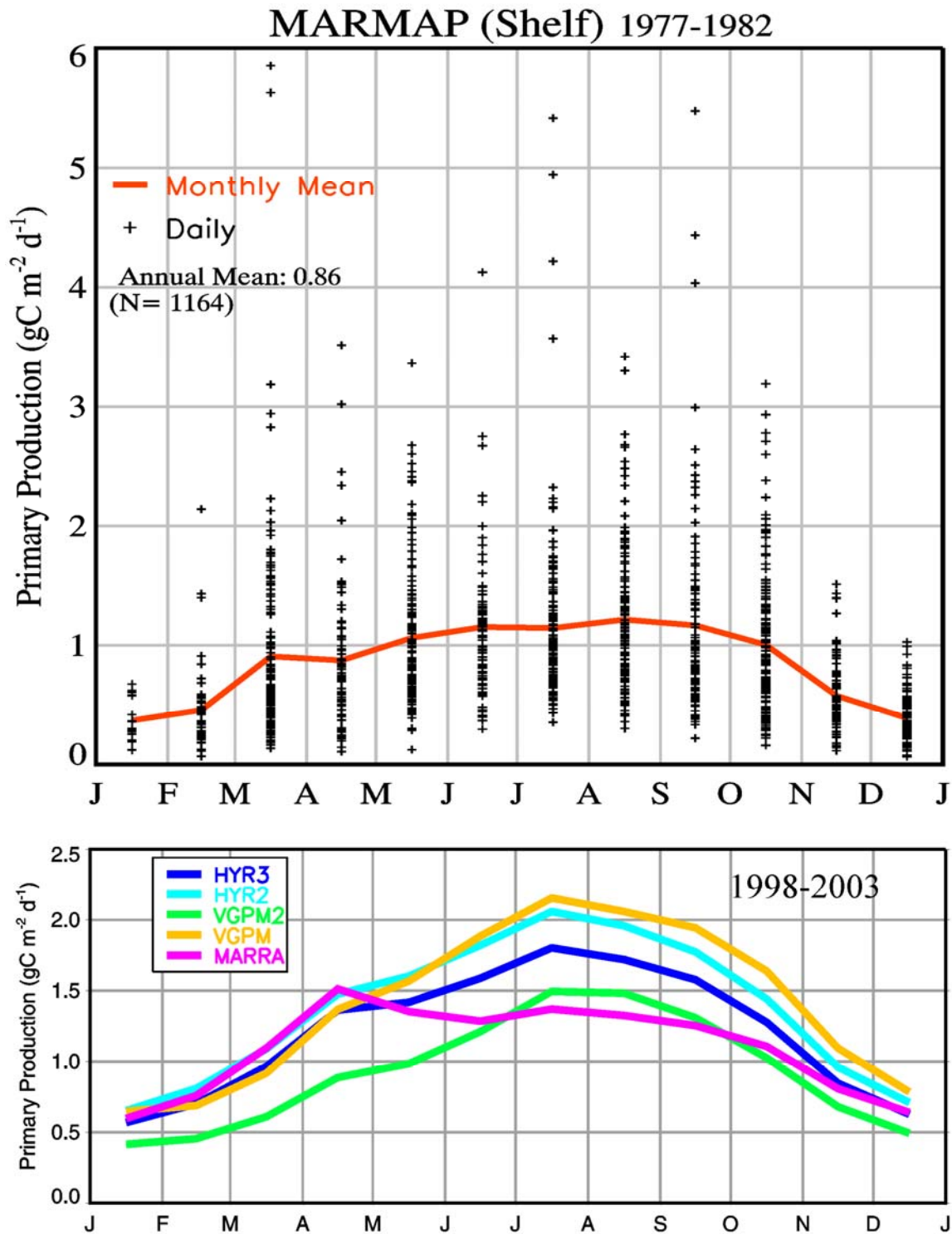


Figure 2.1. Upper panel: The annual primary production cycle for the Northeast U.S. Continental Shelf (MARMAP 1977-1982). Lower panel: Annual primary production cycle derived from satellite data (1998-2003) and productivity models (VGPM - Behrenfeld and Falkowski 1997; VGPM2 - see methods; MARRA - Marra *et al.* 2003; HYR2, HYR3 - Howard and Yoder 1997).

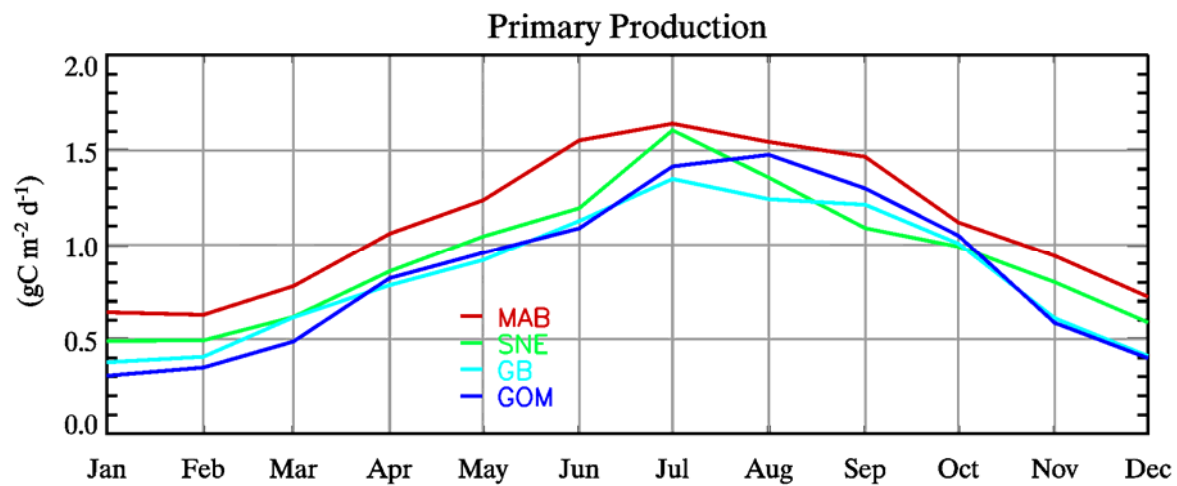


Figure 2.2. Annual cycle of primary production ($\text{g C m}^{-2} \text{d}^{-1}$) for the Mid-Atlantic Bight (MAB), Southern New England (SNE), Georges Bank (GB) and Gulf of Maine (GOM) regions (1998-2000).

3. Bacteria

David D. Dow and John E. O'Reilly (node #2)

Background/Data Sources

In the past two decades numerous studies have reported on the quantitative significance of energy and matter flows through the “microbial loop”, particularly studies by biological oceanographers interested in nutrient cycling (Pomeroy 2004). While there have been numerous surveys and studies of the phytoplankton primary producers in the NEUS Ecosystem, spatially and temporally comprehensive surveys of the distribution, abundance and metabolic rates of heterotrophic bacterioplankton have not been conducted. Consequently, our estimates of bacterioplankton metabolic rates must be based on indirect methods and on studies and knowledge derived from comparable ecosystems. The primary grazers of bacterioplankton, the microzooplankton, are also poorly characterized for this shelf ecosystem. Together, the bacterioplankton and microzooplankton feeding guilds link dissolved primary production and detritus (particulate organic carbon) to the mesozooplankton. Subsequently, it is available to the living marine resources at higher trophic levels.

Network models such as Ecopath frequently use the detritus compartment to accumulate heterotrophic egestion/excretion energy and sedimented primary production not utilized in the surface mixed layer. In order to process this accumulation of detritus, we added bacteria and microzooplankton guilds (consumption followed by respiration) and transferred a component (secondary production of microzooplankton) to the grazing food chain via mesozooplankton ingestion (mesozooplankton are assumed to be omnivores).

In the EMAX network models the detritus node is particulate organic carbon (POC) processed by vertebrate/invertebrate detritivores which consume the POC and attached bacteria/protozoa. Since bacteria utilize labile and semilabile dissolved organic carbon (DOC), the tacit assumption is that bacterial extracellular enzymes convert the POC to DOC before it is taken up by the bacteria. Even though DOC represents a large nonliving organic carbon pool in the water column, much of it is refractory, and since we do not know its bioavailability to bacteria, the EMAX network models did not explicitly model a node for DOC. Moreover, the operational definition of DOC is the organic matter which passes through a 0.7 μm glass fiber filter, and includes small particles and colloidal organic carbon, making it difficult to distinguish POC and DOC assimilation efficiencies.

In the EMAX networks, bacteria utilize and respire POC. The photoassimilated dissolved organic carbon released by phytoplankton and bacterioplankton are fed upon by microzooplankton prior to a transfer pathway to mesozooplankton. This is obviously a simplification of what occurs in the “microbial loop” which has multiple transfer steps between different size classes of phytoplankton and a variety of microbial heterotrophs (Calvet and Saiz 2005). There is a debate in the literature about whether the “microbial loop” is a sink for POC and DOC (respiration of primary production and storage of carbon in inactive microbial cells) or a source of carbon to the grazing food chain through mesozooplankton acting as omnivores (Ducklow 1994). The assimilation efficiency of bacteria for DOC and POC is often assumed to be 50%, but it may be lower due to the refractory nature of much of the DOC and components of the POC (Pomeroy 2001).

Quantitative Approach for Estimates

Since we had estimates of the phytoplankton biomass and primary production from satellite data for the four subregions of the NEUS Ecosystem, it was assumed that bacterial secondary production (BP) should be roughly 10% of the primary production (PP). We adjusted the consumption of the bacterioplankton node so that the BP:PP ratio = 0.10 (Table 3.1). This is lower than the commonly assumed BP:PP range of 0.15 to 0.30 (Pomeroy 1979; Cole *et al.* 1988; Pomeroy 2001). The outcome of this adjustment was that bacterial consumption was roughly 40% of the net production (PP). This is similar to the value reported in Calbet (2001) for the consumption of primary production by micro- and mesozooplankton in coastal waters. Bacterioplankton have a critical role in processing the excretion (DOC) and egestion (POC) from the other living nodes in the EMAX network. The resultant transfer of recycled carbon from the microbial loop to the grazing food chain improves the overall transfer efficiency of the network energy flow. Given this important trophic role for bacterioplankton, the fact that they might consume 40% of PP via either direct or indirect energy pathways in the EMAX model is not unreasonable.

The other key assumptions were: bacterial gross growth efficiency (GGE) = 0.24; growth rate (P:B) = 0.25 per day; Assimilation Efficiency (AE) = 0.80 and carbon x 10 = wet weight (Bratbak and Dundas, 1984). These assumptions permitted the estimate of the bacterial biomass from BP and growth rate, while the various energy flow ratios (C:B, R:B, R:P, etc.) can be computed using the GGE and AE values. Ducklow (2000) reported an average bacterial growth rate of 0.3 d^{-1} for the eastern North Atlantic spring phytoplankton bloom, and lower rates ($0.05\text{--}0.25 \text{ d}^{-1}$) for other open sea regions. Reinthaler and Herndl (2005) reported a mean bacterioplankton growth rate of $0.2 \pm 0.3 \text{ d}^{-1}$ for the southern North Sea. Assuming an average bacterial growth rate of 0.25 d^{-1} applies to the NEUS Ecosystem, then the standing stocks of bacterioplankton biomass in the GOM would be estimated at 0.345 g C m^{-2} . This equates to approximately 17% of the phytoplankton standing stock (2.011 g C m^{-2}), based on an average vertically integrated chlorophyll value of $52.73 \text{ mg Chl m}^{-2}$ and a phytoplankton carbon:chlorophyll ratio of 40:1.

Del Giorgio and Cole (2000) summarize estimates of bacterial net growth efficiency for a variety of marine systems, reporting a mean value of 0.27. This net growth efficiency (NGE) is slightly lower than our value of 0.30. The growth rate assumption yields an annual P:B = 91.2 which is slightly lower than the value of 100 for bacteria given in Pomeroy (2001). EMAX doesn't use DOC as a food source for bacterioplankton, but Ducklow and Shia (1992) estimate a bacterial conversion efficiency of 20% for DOC and 50% of bioavailable organic matter (like algal exudate). Since the continental shelves have a greater percentage of bacteria attached to particles (POC) than the free living bacteria which dominate the open ocean, we assumed that bacterial enzymes convert the POC to DOC which is consumed by the bacterioplankton. Since EMAX has the bacterioplankton consuming detritus from egestion by the other living nodes, algal exudate and the phytoplankton that sediment out of the euphotic zone, we assumed that the AE = 0.80. The quality of the available POC and DOC seems to determine the AE value and the assimilation efficiency differs between the carbon (used for respiration) and nitrogen (used for growth and cell division). Thus the literature had a broad range of values for AE. The AE for the different heterotrophic nodes determines the rates at which this POC flows into detritus and is shown by the Lindeman Spine in the network output. Our balanced network flow models had high AE values which minimized this POC production.

The resulting biomass of bacterioplankton was 0.345 g C m^{-2} with a production of $0.0863 \text{ g C m}^{-2} \text{ d}^{-1}$ for the Gulf of Maine (GOM). The carbon values were converted to wet weight (see Table 3.2) based on the following conversion factors: carbon $\times 0.5$ = dry weight; and dry weight $\times 0.20$ = wet weight (or carbon wt. $\times 10$ = wet weight). The estimated wet weight biomass is 3.452 g m^{-2} and annual production is $315.026 \text{ g m}^{-2} \text{ y}^{-1}$. This implies that the annual P:B ratio = 91.3 (which lies between the 163 for phytoplankton and 72 for microzooplankton). Given the GGE and AE assumptions, the net growth efficiency (NGE) is 0.30 which implies that respiration is 70% of the assimilated energy, with the other 30% going to secondary production. NGE values in the literature generally lie between 0.20 and 0.40 (Reinthal and Herndl, 2005). The choice of the NGE value has a major role in determining whether the microbial loop is a sink for primary production or a link to the grazing food chain. The bacterioplankton consumption was $0.360 \text{ g C m}^{-2} \text{ d}^{-1}$ with respiration representing $0.201 \text{ g C m}^{-2} \text{ d}^{-1}$ and production $0.086 \text{ g C m}^{-2} \text{ d}^{-1}$. The energetic ratios were: C:B = 1.042; P:B = 0.250 (assumption); R:B = 0.583; and P:R = 0.429. Table 3.1 provides values reported for some other oceanic systems: coastal embayment (Narragansett Bay, NB) and open ocean (North Atlantic Bloom Experiment, NABE). Most of the information on the structure/function of the bacterioplankton community is from studies in estuaries and the open ocean. We assumed that the metabolic activity of bacterioplankton in continental shelf water lies somewhere between the extremes of this gradient. Table 3.1 provides an overview of the underlying assumptions used to estimate bacterial production and biomass, plus the diagnostic energy flow ratios used in the EMAX network model.

In NB the reported gross primary production is $1.49 \text{ g C m}^{-2} \text{ d}^{-1}$ and phytoplankton biomass is 3.8 g C m^{-2} . NB net primary production ($0.87 \text{ g C m}^{-2} \text{ d}^{-1}$) is comparable to our estimate for GOM ($0.9 \text{ g C m}^{-2} \text{ d}^{-1}$), while the standing crop biomass is higher than our estimate for the GOM ($2.01 \text{ g C m}^{-2} \text{ d}^{-1}$). The NABE model is based on values averaged over a 20 day spring bloom/post-bloom period, and we presume that these daily values do not represent the yearly average which is lower in the open ocean than on continental shelves. In NB the standing crops (g C m^{-2}) are 1.2 for pelagic bacteria and 0.5 for microzooplankton, compared to NABE values of 0.1 for bacteria and 0.5 for microzooplankton. The bacterioplankton biomass in the GOM is 0.345 g C m^{-2} which lies along the gradient between NB and the NABE.

In EMAX we partitioned assimilated energy 70% to respiration and 30% to secondary production, which is much different than that reported for the open ocean where respiration is 90% and secondary production is 10% (Ducklow and Carlson, 1992). Our values were chosen to have the bacterioplankton be a link through microzooplankton to the grazing food chain, while the oceanic values assume that the microbial loop is a sink for DOC with most of the carbon being respired. In order to eliminate POC accumulation from the egestion emanating from the other living nodes in EMAX, we assumed that the 70% respiration component would remove this detritus. The secondary production component (30%) provides the link to the grazing food chain.

Del Giorgio and Cole (2000) summarized measurements of bacterial growth efficiency (BGE) for a number of marine systems. In their work, BGE is the ratio of bacterial production to bacterial respiration plus production ($\text{BGE} = \text{BP}/[\text{BR} + \text{BP}]$), and they reported a mean BGE value of 0.27 for coastal areas. This value implies that 73% of the carbon uptake is respired and 27% is retained as organic carbon production, yielding a respiration:production ratio of 2.7 and a consumption:production ratio of 3.7. The bacterial carbon demand (BCD) is BP/BGE and provides an estimate of the heterotrophic consumption in relation to the net primary production.

Since we ignored the DOC component of bacterial consumption, our BCD estimates will be biased high. An exception is bacterial uptake of phytoplankton dissolved production, for which we assumed 100% assimilation efficiency.

Only a portion of the POC is bioavailable to bacteria, but we assumed that all the dissolved primary production was utilized by them. Since we did not know the percentage of POC bioavailability, we adjusted the bacterial respiration rate in order to consume the “apparent detritus production” to prevent it from accumulating or having to export a large fraction out of our system boundaries. Since the network models we used balance the flows through the detritus component, one has to develop a way to consume the “apparent detritus production”. We decided not to explicitly incorporate the DOC pool in the energy flow pathway, even though it represents a large non-living carbon pool (15 times the POC and 75 times the phytoplankton carbon) of unknown bioavailability in the “microbial loop”. We incorporated POC in the EMAX energy flow, since it was a component of the diet matrix for a number of feeding guilds (or nodes) in the network. All of the material egested in the different heterotrophic nodes contributes to the POC pool.

Results

The GOM data in Table 3.1 shows the estimates that were used in EMAX. We assumed a gross growth efficiency of 24% for EMAX (Table 3.2), noting that Del Giorgio and Cole (2000) reported 20%. The ratio of heterotrophic secondary production:primary production in EMAX is 0.10 (assumption), whereas Ducklow (2000) and Reinthaler *et al.* (2005) report a value of 0.15 and Cole *et al.* (1988) report a range between 0.20-0.30.

As shown in Table 3.2, EMAX used fairly high values of Assimilation Efficiency (AE, 80%) and Gross Growth Efficiency (GGE, 24%) since we wanted to prevent the accumulation of detritus or its export out of the system. We assumed that net primary production is approximately balanced by the heterotrophic community respiration on the NEUS Continental Shelf Ecosystem. If one used the values suggested in the literature (AE < 50% and GGE = 20%), then the bacterioplankton would consume the net primary production and none would be available for transfer to the grazing food chain that supports living marine resources (LMRs). EMAX assumed that the microbial food web was a link to the grazing food chain. Using these lower values for AE and GGE would lead to the ecosystem being net heterotrophic ($P \ll R$) and runs counter to field observations, but supports the notion of the “microbial loop” being a carbon sink. This issue is discussed at greater length by Williams (2000) who estimated that bacteria provide 40% of the heterotrophic community respiration. The implications of bacterial GGE values on bacterial consumption of DOC is explored by Ducklow (2000) and Del Giorgio and Cole (2000). Nagata (2000) estimated that bacterial consumption of DOC corresponded to 42% of net primary production, while Williams (2000) estimated that this value was 50%. The issue of the P versus R balance in the water column is discussed by Del Giorgio and Williams (2005).

The EMAX bacteria/phytoplankton biomass and productivity ratios listed in Table 3.1 are similar to those in the literature. Therefore, even if there are some problems with our carbon to wet weight conversions, our scaling between bacteria and phytoplankton seems to be reasonable. Since a significant fraction of the bacterial biomass in oligotrophic, oceanic areas is metabolically inactive, there is much variation in the C:B, R:B, and P:B ratios in the literature, with a wide range of values as one moves from estuarine to open ocean regions. We did not have

the regional data necessary to estimate the metabolically active bacterial biomass, so we used an approach based on literature values to bound the bacterial biomass and rates.

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Table 3.1. Comparison of biomass and rate parameters reported for phytoplankton and bacterioplankton in Narragansett Bay (NB) and North Atlantic Bloom Experiment (NABE) with estimates derived for the Gulf of Maine (GOM).

Parameter	Units	NABE	NB	GOM EMAX
Phytoplankton Biomass	g C m^{-2}		3.8	2.011
Net Primary Production	$\text{g C m}^{-2} \text{ d}^{-1}$	0.87	0.87	0.90
Gross Primary Production	$\text{g C m}^{-2} \text{ d}^{-1}$		1.49	1.124
Phytoplankton Production:Biomass				0.447
Bacteria Biomass	g C m^{-2}	0.1	1.2	0.345
Bacteria Consumption – detritus	$\text{g C m}^{-2} \text{ d}^{-1}$		1.32	0.360
Bacteria Consumption – DOC	$\text{g C m}^{-2} \text{ d}^{-1}$		0.035	
Bacteria Consumption – total	$\text{g C m}^{-2} \text{ d}^{-1}$		1.35	0.360
Bacteria Respiration	$\text{g C m}^{-2} \text{ d}^{-1}$	10.6	0.0863	0.201
Bacteria Production	$\text{g C m}^{-2} \text{ d}^{-1}$	2.2	0.482	0.0863
Bacteria Production:Biomass			0.40	0.25
Bacteria Production:Respiration			5.59	0.429
Bacteria Consumption:Production				4.166
Microzooplankton Standing Crop	g C m^{-2}	0.5	0.5	0.261

Table 3.2. Bacterioplankton conversions/comparisons.

Parameter	GOM EMAX	Reported Values	Reference
Assimilation Efficiency	80%	50% 25-30% (on natural DOC)	Pomeroy & Wiebe 1993 Pomeroy & Wiebe 1993
Gross Growth Efficiency	24%	20%	Del Giorgio & Cole 2000
g C: Wet Weight	1:10	1:10	Bratbak & Dundas 1984
mg C:mg dry	0.5	0.5	Bratbak & Dundas 1984
mg dry:mg wet	0.2	0.2	Bratbak & Dundas 1984
mg C:mg wet	10	10	Bratbak & Dundas 1984
Heterotrophic:Primary Production	0.10	0.15 0.15 0.20-0.30	Ducklow 2000 Reinthalder <i>et al.</i> 2005 Cole <i>et al.</i> 1988
Bacteria:Phytoplankton Biomass	0.17	01-0.6 0.16 0.27	Ducklow 2000 Pomeroy 1979 Pomeroy 2001

4. Microzooplankton

David D. Dow, John E. O'Reilly and John R. Green (node #3)

Background/Data Sources

The microzooplankton group includes holoplankton (protozoa, ciliates, flagellates, copepod nauplii, etc.) and meroplankton (larval stages of benthic invertebrates: trochophores, veligers, etc.). This diverse assemblage has a range of biomass and rate values. For example, in the southeast Bering Sea the protozoan component had a biomass of 10 Mg km^{-2} , a P:B ratio of 72 and a C:B ratio of 144, while the other holoplankton/meroplankton biomass was 13.3 Mg km^{-2} , P:B was 9 and C:B was 27 (Ciannelli *et al.* 2004). In EMAX it was assumed that the microzooplankton were primarily composed of protozoans which have a boom and bust life history strategy that tracks the abundance of their prey (Reid *et al.* 1993). The microzooplankton in the EMAX model feed on bacteria (40% of diet), small phytoplankton (15%), detritus (35%) and other microzooplankton (10%). This diet composition reflects the reality that in nature they consume a wide variety of microautotrophs/heterotrophs (and cannibalize one another). Stimulated by new nitrogen, the spring phytoplankton bloom is often dominated by net plankton (diatoms) which are consumed primarily by mesozooplankton (large and small copepods). Microzooplankton grazing also occurs as a minor component. During the summer stratified period when recycled nitrogen maintains primary productivity, the phytoplankton is dominated by smaller nanoplankton (i.e., dinoflagellates, microflagellates, non-colonial diatoms, etc.) which are grazed by microzooplankton. Microzooplankton grazing of bacteria is the primary link between the microbial loop and grazing food chain.

Quantitative Approach for Estimates

The microzooplankton (MZ) biomass fluctuates seasonally like the phytoplankton biomass, since it is controlled by food resources and grazing. In the EMAX model the food resources are small planktonic autotrophs/heterotrophs and the grazers are mesozooplankton (three nodes). Since we didn't have any independent data on protozoan biomass and rates on the Northeast Continental Shelf, we decided to relate the MZ biomass (in carbon units) to that of phytoplankton (in carbon units) based on Figure 3 in Caron *et al.* (1990) which showed a relationship (log-log) between ciliate and phytoplankton biomass. We assumed that MZ biomass was 0.13 of the phytoplankton biomass, similar to values for unfertilized North Sea mesocosms (Baretta-Bekker, 1994) and Narragansett Bay (Monaco, 1997). Given the boom and bust life history strategy of protozoans, we assumed that their annual biomass would be a relatively small fraction of the annual phytoplankton biomass. As described in the Phytoplankton Section of this document, we had satellite data available to estimate phytoplankton biomass (conversion from chlorophyll *a* to carbon) in the euphotic zone. The phytoplankton biomass was revised to include its distribution throughout the water column, so that it could be used to estimate the MZ biomass. The phytoplankton biomass was $2.0114 \text{ g C m}^{-2}$ which resulted in a microzooplankton biomass of $0.2615 \text{ g C m}^{-2}$. These values are shown in Table 4.1. We converted from carbon to dry weight and then to weight wet using the conversion factors in Sherr and Sherr (1984). The dry/wet weight conversion factor was 0.18, while the dry weight/carbon conversion factor was 0.46, yielding a carbon/wet weight conversion factor of 0.0828. Thus the

estimated wet weight biomass for phytoplankton was 20.1144 g m⁻² and 3.158 g m⁻² for microzooplankton.

We estimated the ratios of the rates (C:P, P:B, R:P) in carbon units on a daily basis and then converted these to wet weight values on an annual basis. The conversion factors and literature sources for these are shown in Table 4.2. The estimated rates of consumption and respiration shown in Table 4.1 are based on a net growth efficiency of 33% (Straile, 1997; Muren *et al.*, 2005); assimilation efficiency of 90%; and P:B ratio of 72 (Pomeroy, 2001). Using these assumptions, 67% of the assimilated energy goes to respiration and 33% to secondary production. Consumption for the microzooplankton is 0.1737 g C m⁻² d⁻¹ and the assimilation value is 0.1563 g C m⁻² d⁻¹. Of the assimilated energy, the respiration is 0.1047 and the secondary production is 0.0516. The growth rate (0.197 per day) was based on the assumption that the MZ biomass turns over every 5 days. The growth rate for microzooplankton was assumed to be much slower than that of phytoplankton and slightly slower than that of bacterioplankton. Table 4.1 compares the consumption, respiration and production rates for EMAX GOM (Gulf of Maine) with that of the southeast Bering Sea (BS), North Atlantic Bloom Experiment (NABE), and Narragansett Bay (NB). The NABE values come from a bloom in the open ocean and thus don't represent daily means from a yearly perspective. In theory continental shelf values should fall somewhere along the gradient from inshore waters (NB) to open ocean (BS and NABE). In general the EMAX GOM P:B, P:R, and C:P ratios lie along this inshore/open ocean gradient. Unfortunately most of the literature values that we found came from either inshore waters or the open ocean, so that we had to assume the continental shelf values lies somewhere between the extreme ends of this gradient.

The European Regional Seas Ecosystem Model (ERSEM) lists the assimilation efficiency (AE) for microzooplankton as 50%, even though the value for heterotrophic nanoflagellates is lower at 20% (Baretta-Bekker *et al.* 1995). The bacterial AE is usually assumed to be 50%, even though it can range as low as 25-30% on natural substrates. The AE is related to the mode of feeding, food quality, and the extent of DOC excretion. Protozoa can have significant excretion losses as DOC (Nagata 2000), which explains the range of variation in the AE values. The EMAX AE value was taken as 90% to reflect Protozoa feeding on bacteria attached to detritus (POC), but not DOC, which can be an important pathway (Nagata 2000). The Gross Growth Efficiency (GGE) for microzooplankton is often taken as 40% (McManus 1991), but in EMAX we used 30% (Straile, 1997; Muren *et al.*, 2005). Thus the GGE lies between that of bacteria (24%) and phytoplankton (80%). The microzooplankton secondary production:primary production ratio varies from 7% (ERSEM Model for North Sea, Baretta-Bekker *et al.* 1995) to 14% (English Channel in August, Newell and Linley 1984). The EMAX P:B ratio was assumed to be 72 (Pomeroy, 2001). The EMAX C:B ratio (daily) was assumed to be 0.66 based on an AE of 90%, which is higher than the English Channel C:B value (0.33 per day, Araujo *et al.*, 2005), but is lower than the Baltic Sea value (1.49 per day, Harvey *et al.* 2003). The EMAX R:B ratio was assumed to be 0.40 per day and should lie somewhere between P:B (0.197 per day) and C:B (0.664 per day). Since DOC release can be a significant component for microzooplankton, our R is actually respiration + excretion (where we don't know the magnitude of E). Thus the R:B ratio might differ from 0.40 (58 per yr) if DOC were addressed in the EMAX network model.

The factor for converting microzooplankton carbon weight to wet weight is a multiplier of 12, based on a g C:g dry weight ratio of 0.46 and g dry:wet weight ratio of 0.18 (Table 4.2). As explained in other Sections, we used slightly different carbon to wet weight conversion factors for phytoplankton, bacterioplankton, and detritus (multiplier of 10). Table 4.1 expresses

the P:B, P:R, and C:P ratios on a daily basis, since microzooplankton have a rapid turnover time. We discuss these as yearly values in the text in order to make the values comparable to those reported for other EMAX nodes, which deal with biota with much longer population turnover times.

Results

It is commonly found that when one compares photosynthesis to respiration in the oceanic water column, the ocean appears to be net heterotrophic ($P < R$; Pomeroy and Wiebe 1993; del Giorgio and Williams 2005). This suggests that either there are methodological problems in measuring primary production and community respiration, or the spatial/temporal coupling is offset and results in biases as one goes from seasonal samples to estimating annual averages. Network analysis balances inputs and outputs from a node so that secondary production of the prey node or food assimilated by the predator node is artificially balanced by respiration, secondary production, net exports/imports, biomass accumulation and harvest removal. Ecopath with Ecosim computes respiration by difference, since it is based on production from the donor node driving the consumption in the receiving node. EcoNetwrk, on the other hand, incorporates respiration as a parameter and is consumption driven. Thus in network models there is a relationship between C:B, R:B, and P:B such that in the balanced models they are different from the input values.

Table 4.2 indicates that the GGE and microzooplankton:phytoplankton biomass (0.13) and productivity (0.07) ratios used in EMAX are similar to those from the literature. This suggests that we got the scaling right in extrapolating from phytoplankton to microzooplankton. We choose a high AE (90%) in EMAX to help transfer the bacterial production efficiently to copepods for transfer up the grazing food chain. Since EMAX did not include DOC as a node, a lot of the bacterial production stems from DOC use beyond just the phytoplankton dissolved production. Therefore, we used higher assimilation efficiencies as compensation to link the microbial food web to the grazing food chain. Our microzooplankton secondary production:phytoplankton production ratio is slightly lower than those reported in the literature.

In EMAX the mesozooplankton biomass ($108.4 \text{ g wet wet m}^{-2}$) is much larger than the microzooplankton biomass ($3.2 \text{ g wet wet m}^{-2}$), but this is partly compensated for by a higher P:B ratio (72) in microzooplankton compared to the 3 mesozooplankton nodes (P:B range from 20-40). It is assumed that the nauplii and copepodites stages of mesozooplankton reside in the small copepod node and thus the microzooplankton are primarily protozoans. Protozoans can grow almost as rapidly as their bacterial prey which leads to a high P:B ratio, but their boom and bust life history strategy probably results in a much lower average biomass than that of mesozooplankton. Unfortunately traditional zooplankton sampling nets destroy the fragile protozoans, so we lack a monitoring database to evaluate the ecological importance of this microzooplankton group.

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Table 4.1. Comparison of biomass and rate parameters reported for microzooplankton in the southern Bering Sea (BS), North Atlantic Bloom Experiment (NABE) and Narragansett Bay (NB) with estimates derived for the Gulf of Maine (GOM).

Parameter	Units	BS	NABE	NB	GOM
Biomass	g C m^{-2}	1.1	1.2	0.45	0.261
Consumption	$\text{g C m}^{-2} \text{d}^{-1}$	2.0	13.9	0.52	0.174
Respiration	$\text{g C m}^{-2} \text{d}^{-1}$		7.6	0.19	0.105
Production	$\text{G C m}^{-2} \text{d}^{-1}$	0.67	1.9	0.17	0.052
Production:Biomass		0.05	1.6	0.37	0.20
Production:Respiration		0.25	0.89	1.3	0.49
Consumption:Production		2.98	7.3	3.05	3.37

Abbreviations:

BS: Southeastern Bering Sea

NABE: North Atlantic Bloom Experiment

NB: Narragansett Bay

GOM: Initial Gulf of Maine EMAX Input

Table 4.2 Microzooplankton conversions/comparisons.

Parameter	GOM EMAX	Reported Values	Reference
mg dw: mg C		2.2	Sherr & Sherr 1984
mg ww: mg dw		5.56	Sherr & Sherr 1984
mg C: mg wet wt	12.1	12.5	Sherr & Sherr 1984
Assimilation Efficiency	90%	20-50%	Baretta-Bekker <i>et al.</i> 1995
Gross Growth Efficiency	30%	40%	McManus 1991
Heterotrophic:Primary Production	0.30	0.07 ERSEM	Baretta-Bekker <i>et al.</i> 1995
		0.11 North Sea	Baretta-Bekker <i>et al.</i> 1995
		0.14 English Channel	Newell and Linley 1984
Microzoo:Phytoplankton Biomass	0.13	0.11	Baretta-Bekker 1994
		0.12 Narragansett Bay	Monaco <i>et al.</i> 1997
		0.99 English Channel	Pomeroy 2001

5. Copepods (large and small)

John R. Green and Joseph M. Kane (nodes #5 and 4)

Background

The large copepod species were defined as the V and VI copepodites stages of *Calanus finmarchicus*, *Metridia lucens*, and *Centropages typicus*. The small copepods were defined as stage I-IV copepodites of the large copepod species and the I-VI copepodites stages of *Centropages hamatus*, *Pseudocalanus* spp., *Temora longicornis*, *Paracalanus parvus*, *Nannocalanus minor*, and *Clausocalanus arcuicornis*. The ten taxa included here make up, on average, 63.3 % of the total zooplankton organisms taken during the six seasons for the 1995 through 2000 period. All ten taxa were present at some sampled sites during all six seasons with mean seasonal abundances ranging from 5 to 20,000 /100 m³. Maximum abundances for each taxon exceeded 100,000/100 m³ at some locations during the period. The highest recorded station abundance (1,260,000/100 m³) was recorded in early autumn for the copepod *Centropages typicus*.

Data Sources and Abundance Estimates

The mean abundance (#/10m²) of large copepods and small copepods were calculated for bimonthly subsets (Jan-Feb, Mar-Apr...) of the ECOMON zooplankton time series from the 1996-2000 period (Table 5.1). Plankton samples were collected seasonally on two types of cruises: 1) broadscale surveys dedicated to plankton where sampling was done at standard or randomly selected stations spaced approximately 8-35 km apart; and 2) trawl and dredge surveys where plankton stations were selected from a stratified random plan at locations uniformly distributed over the region. Samples were all collected with a 61 cm bongo frame fitted with a 0.333 mm mesh net towed obliquely to a maximum depth of 200 m or 5 m from the bottom and back to the surface. A digital flowmeter was suspended in the center of the bongo frame to measure volume of water filtered during the tow. Specimens were preserved in 5% formalin. Samples were then reduced to approximately 500 organisms by subsampling with a modified box splitter. Zooplankton was sorted, counted, and identified to the lowest possible taxon at the Polish Sorting and Identification Center.

Total counts of zooplankton within the ecosystem were highest during late summer when dense concentrations pervade throughout the MAB and within the shallow waters of the SNE and GB subregions. These high aggregations persist through late autumn, nearly disappear during winter, and began to reappear during early spring. Overall abundance was lowest in the GOM region, but there was a band of high abundance along the southwestern coastal zone that was present in all seasons except winter.

Samples were numerically dominated by three copepod species: *Calanus finmarchicus*, *Centropages typicus*, and *Pseudocalanus minutus*. These three species, on average, accounted for 46% of the total number of organisms present in our samples. Of the three species, *C. typicus* was the most abundant of the zooplankton community. This warm water omnivore dominates ecosystem waters from late summer through early winter. Its density was high year-round in the southern half of the region and became elevated in the more temperate northern half of the ecosystem during late summer. Ecosystem abundance peaks in late autumn when the copepod abundance is above 10,000/100 m³ throughout most of the region.

The herbivores *Calanus finmarchicus* and *Pseudocalanus minutus* utilize the spring phytoplankton bloom and dominate early and late spring samples. Both species have similar annual abundance cycles but differ in their spatial distribution. *Pseudocalanus* spp. abundance rises sharply in early spring when it concentrates in coastal areas of the MAB, throughout SNE, and the western and eastern margins of the GOM. Peak seasonal abundances occurred in late spring with high values found throughout SNE, in the more shallow waters of GB, and along coastal GOM. *C. finmarchicus* abundance was high year-round in the GOM and on GB from early spring through late summer. Dense concentrations of this copepod were also found in the offshore waters of SNE and the MAB in late spring and late summer. Abundance was low year-round in the coastal waters of these latter two regions.

The annual abundance cycle and spatial distribution of *Metridia lucens* was very similar to *Calanus finmarchicus*, though overall abundance levels were much lower. Density is highest during late spring and the largest concentrations were usually found in the western GOM and along the outer shelf of the MAB and SNE subregions. Abundance was low year-round in southern coastal waters and within the central shoals of GB.

The copepod *Centropages hamatus* reached peak abundance during the late summer when dense concentrations formed in the central shoals region of GB and persisted there through late autumn. High levels were also found in MAB and SNE coastal waters during early and late spring. The copepod was sparsely distributed year-round in the GOM and during the latter half of the year in the MAB and SNE subregions.

Mean abundance of *Acartia* spp. peaked during late summer when they concentrated in shallow coastal waters throughout the ecosystem. Numbers remained high inshore through late autumn in the southern half of the ecosystem. They became scarce in the GOM during winter and early spring. *Temora longicornis* mean abundance also peaked during late summer when high concentrations of the copepod were found scattered in shallow waters throughout the ecosystem. It also was very scarce in the GOM during the colder months.

Oithona spp. were captured year round in nearly all samples from the ecosystem. However, there was no strong seasonal cycle and only relatively large concentrations were found scattered throughout the MAB and SNE regions. It should be noted that the abundance levels of this comparatively small copepod species is underestimated because it is not quantitatively caught with the nets used in our surveys. *Paracalanus parvus* abundance was at its maximum during late autumn when high concentrations were found across SNE and GB. It was present year-round in the SNE and MAB subregions and became very rare in GOM and GB waters during the spring seasons.

Biomass Estimates

Copepod abundance by size group was converted to biomass using the length to wet weight (W) equation given by Pearre (1980):

$$(EQ. 5.1) \quad W = 0.08810L^{2.8514}$$

This equation is based on Petipa (1957) and others using prosome lengths (L) of various copepod species obtained from the literature (Table 5.1).

Production

Copepod production was calculated according to Huntley and Lopez (1992) using the formula:

$$(EQ. 5.2) \quad P = B \cdot 0.0445e^{0.111T}$$

where P is production; B is copepod biomass^{-m2}; and T is mean temperature. Mean temperatures are derived from integrated CTD temperature profiles taken at each station (Table 5.2).

Consumption

Feeding rates were derived from Pafenkofer (1976) based on the daily weight-specific filtering rate for a calanoid copepod, *Calanus helgolandicus*. This rate, 0.20 times biomass/day, was scaled to an annual consumption rate for both copepod size groups. Thus, both groups were assumed to have the same consumption rates relative to body size.

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Table 5.1. Estimates of seasonal biomass for large and small copepods (grams dry weight 10 m⁻²) by EMAX Region 1996-2000.

Large Copepods (derived from lengths using Pearre 1980)				
Season	MAB	SNE	GBK	GOM
Jan-Feb	6.08	5.36	4.34	9.14
Mar-Apr	9.34	9.84	12.82	21.88
May-Jun	9.04	17.30	22.37	43.81
Jul-Aug	-	17.05	13.10	54.22
Sep-Oct	3.34	8.32	18.45	44.36
Nov-Dec	3.54	11.35	14.40	35.73
AVG	5.23	11.54	14.25	34.85

Small Copepods (derived from lengths using Pearre 1980)				
Season	MAB	SNE	GBK	GOM
Jan-Feb	1.90	1.75	2.06	1.01
Mar-Apr	4.18	9.18	11.50	11.82
May-Jun	7.66	14.11	17.72	17.13
Jul-Aug	-	7.45	7.11	10.42
Sep-Oct	1.44	2.29	7.51	5.00
Nov-Dec	3.32	3.24	4.03	4.02
AVG	3.08	6.34	8.32	8.23

Table 5.2. Estimates of seasonal P, B and T for large and small copepods by EMAX Region 1996-2000.
 B = biomass units = g dry wt 10 m⁻²; T = mean water column temperature 1996-2000, <200M; P = production g dry wt 10 m⁻² day⁻¹.

Large Copepods												
Season	MAB B	MAB T	MAB P	SNE B	SNE T	SNE P	GBK B	GBK T	GBK P	GOM B	GOM T	GOM P
Jan-Feb	6.08	8.1	0.66458	5.36	6.8	0.508316	4.34	6.1	0.381461	9.14	5.8	0.777755
Mar-Apr	9.34	7.4	0.946073	9.84	6.1	0.859093	12.82	5.6	1.063897	21.88	5.1	1.71384
May-Jun	9.04	12.2	1.552212	17.30	9.8	2.286007	22.37	9.0	2.694004	43.81	6.6	4.041832
Jul-Aug	-	11.5		17.05	14.2	3.673063	13.10	13.4	2.586063	54.22	9.6	6.964496
Sep-Oct	3.34	19.9	1.355482	8.32	15.8	2.147429	18.45	13.5	3.678572	44.36	9.4	5.601424
Nov-Dec	3.54	15.7	0.898125	11.35	13.6	2.280166	14.40	11.9	2.391141	35.73	8.5	4.081472
AVG			1.08			1.96			2.13			3.86

Small Copepods												
Season	MAB B	MAB T	MAB P	SNE B	SNE T	SNE P	GBK B	GBK T	GBK P	GOM B	GOM T	GOM P
Jan-Feb	1.90	8.1	0.206996	1.75	6.8	0.165763	2.06	6.1	0.181452	1.01	5.8	0.085758
Mar-Apr	4.18	7.4	0.42357	9.18	6.1	0.801963	11.50	5.6	0.954569	11.82	5.1	0.925576
May-Jun	7.66	12.2	1.3146	14.11	9.8	1.864271	17.72	9.0	2.133817	17.13	6.6	1.580857
Jul-Aug	-	11.5		7.45	14.2	1.605211	7.11	13.4	1.403629	10.42	9.6	1.338492
Sep-Oct	1.44	19.9	0.584923	2.29	15.8	0.590272	7.51	13.5	1.497967	5.00	9.4	0.630965
Nov-Dec	3.32	15.7	0.842071	3.24	13.6	0.65012	4.03	11.9	0.669785	4.02	8.5	0.459443
AVG			0.67			0.95			1.14			0.84

6. Gelatinous Zooplankton

John R. Green (node #6)

Background

Gelatinous zooplankton are common constituents of plankton samples. They can be locally very abundant and have significant predatory impact on the composition of the plankton community (Reeve and Walter, 1978). As considered here, gelatinous zooplankton are a taxonomically diverse group that includes the Cnidaria (both the medusae and hydrozoans); the Ctenophores (comb jellies); the colonial Siphonophores; and the colonial Salpidae. All are characterized by a high water content in body tissues that causes significant distortion and shrinkage upon preservation, and by delicate structures that can be fragmented or extruded during capture, making identification and enumeration for abundance estimates extremely difficult and uncertain.

Biomass Estimates

Gelatinous zooplankton biomass was estimated from 60 cm bongo tows with 333 mm mesh nets taken on NEFSC monitoring cruises from 1996-2000. Mean abundances per m³ for each station are the calculated mean of the abundance for each stratum sampled. These were done for six 2-month periods for all the main gelatinous zooplankton groups (Table 6.1). Mean station abundance was multiplied by the sampling depth to calculated no./m².

Individual group biomasses were calculated using the following relationship (Reeve and Walter 1976):

$$(EQ. 6.1) \quad \text{Log DW} = 2.65 * \text{Log L}$$

Where DW is dry weight (g) and L is length (mm). This relationship was established for ctenophores and is assumed to be similar enough for all other gelatinous zooplankton groups such that we used it for all these zooplankton taxa. A mean length of 1.3 mm was assumed for this calculation. Total biomass for all groups was then integrated into an annual average, summed across all gelatinous zooplankton taxa, and then converted to g wet weight per m⁻². Conversion to wet weight from dry weight was approximated from Pages (1997), with DW = 4.48% of WW. Estimates for all four regions are given in Table 6.2.

Production Estimates

Gelatinous zooplankton production was scaled from estimates derived from a study of Ctenophore trophodynamics from the Caribbean (Persad *et al.* 2003). Rates from that study were adjusted for EMAX purposes using a Q10 rule of 2 (i.e., temperature correction of rate processes, with a halving or doubling for each change in temperature of 10°C) to approximate the difference in temperature conditions and the seasonal cycle of prey abundance found in the coastal Northeast Atlantic Ocean.

Upon further reflection, these production estimates were slightly modified to account for depth patchiness, vertical stratification of distribution, seasonality, and the bloom nature of these

organisms. To do so, we adjusted the production value to fall within the range of previously reported (literature) gelatinous zooplankton P:B ratios, resulting in a P:B ratio of ~ 40.

Consumption Estimates

Gelatinous zooplankton consumption rates were scaled to the results of Reeve and Walter (1976). As with production, these estimates were modified to account for depth patchiness, vertical stratification of distribution, seasonality, and the bloom nature of these organisms. Reeve and Walter (1976) estimate a clearance rate of approximately 17% body weight per day. Scaling to other nodes and the Reeve and Walter estimate, our calculations assumed an adjusted clearance rate of approximately 40% body weight per day, which was then annualized. This gives a C:B ratio value of ~146, well within the range of other reported values for similar organisms. This also gives a C:P of 3.5-3.7, a reasonable value and consistent with similar nodes at this trophic level.

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Table 6.1. Estimates of gelantious zooplankton group abundances (no. 10 m⁻²). The averages are presented for each of six 2-month seasons and as an integrated annual estimate. These estimates are for each region and were used to calculate biomass estimates.

Siphonophores	EMAX Regions			
	MAB	SNE	GB	GOM
Jan - Feb	304	529	5608	32832
Mar - Apr	3840	5827	1172	13239
May - Jun	22671	17529	5967	10855
Jul - Aug	-	15264	67811	92589
Sep - Oct	5462	23359	10608	72970
Nov - Dec	20260	10683	10918	84336
Total	8756	12199	17014	51137
<hr/>				
Ctenophores				
	MAB	SNE	GB	GOM
Jan - Feb	0	0	0	10
Mar - Apr	0	5	0	0
May - Jun	106	435	0	0
Jul - Aug	-	0	2	18
Sep - Oct	18	85	3	9
Nov - Dec	9	0	118	0
Total	22	88	20	6
<hr/>				
Salps				
	MAB	SNE	GB	GOM
Jan - Feb	669	0	0	75
Mar - Apr	498	1430	19	36
May - Jun	105	186	443	178
Jul - Aug	-	14128	38321	77151
Sep - Oct	79430	42869	29728	25987
Nov - Dec	19062	4866	615	322
Total	16627	10580	11521	17292
<hr/>				
Coelenterata				
	MAB	SNE	GB	GOM
Jan - Feb	83	216	234	1468
Mar - Apr	86	2584	12372	462
May - Jun	8984	29559	43376	10606
Jul - Aug	-	4364	14805	73400
Sep - Oct	5137	5449	1720	14266
Nov - Dec	2342	1459	316	2137
Total	2772	7272	12137	17057

Table 6.2. Total estimate of gelatinous zooplankton biomass for the different EMAX regions. Values are in g m^{-2} .

EMAX Region	Biomass (g m^{-2})
MAB	3.6
SNE	3.9
GB	5.2
GOM	11.0

7. Micronekton

John R. Green (node #7)

Background

Micronekton are the largest sized animals taken in plankton nets, typically having body lengths of 5-10 mm or more. For this study, the micronekton group is considered inclusive of the crustacean groups amphipoda, euphausiacea, mysidacea and similar decapoda captured in plankton nets. Chaetognatha are also included in this group. Compared to copepods, abundance estimates of micronekton from plankton net sampling are relatively low. There are, however, instances of swarming behavior, particularly of gammarid amphipods and euphausiids, when they can dominate plankton biomass. Such events occur on small temporal and spatial scales. It is possible that bongo nets under-sample micronekton due to net avoidance (Angel and Pugh 2000).

Biomass

Micronekton biomass was estimated from abundance estimates from the ECOMON zooplankton time series for the 1996-2000 period. The mean abundances (no./ 10 m²) of micronekton were calculated for bimonthly subsets (Jan - Feb, Mar - Apr...) distinctly for each of the groups listed above.

These estimates of mean abundance were then converted to biomass based upon established size-biomass relationships. Here we assume that most micronekton were roughly equivalent to a common micronekton taxa, the amphipod *Gamarrus* sp. Mean abundance was converted to dry weight from the relationship established in Avery *et al.* (1996), using a mean length of 6 mm which produced a dry weight estimate of 1.2 mg. This average weight was then multiplied by the abundance estimates to obtain a total biomass for each group (Table 7.1).

However, for the chaetognaths group, dry weight was calculated based on the relationship in Sameoto (1971) for the species *Sagitta elegans*. This formula is:

$$(EQ\ 7.1) \quad DW = 0.00097\ l^{2.2365},$$

where DW is dry weight (mg) and l = length. A mean length of 4 mm was used based on laboratory observations, giving a mean dry weight of 0.026 mg. *S. elegans* is the most abundant chaetognath in these plankton samples.

After conversions to biomass were done for each micronekton group, the values were then converted to biomass and integrated into an annual estimate. This was then converted to g wet weight per m⁻². Estimates for all four regions are given in Table 7.2.

Production and Consumption Estimates

Growth was estimated at 0.04 day⁻¹ and consumption at 0.10 day⁻¹ based on an assumption growth similar to that of juvenile cod of approximately the same size (Peck *et al.* 2003). These values were then scaled to provide an annual estimate.

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Table 7.1. Estimates of micronekton abundance. Units are in Number 10 m⁻² unless otherwise noted. The averages are presented for each of six 2-month seasons and as an integrated annual estimate. DW = dry weight, WW = wet weight.

	EMAX Region			
	MAB	SNE	GB	GOM
Amphipods				
Jan - Feb	4432.8	5555.8	1869.9	3413.0
Mar - Apr	2790.7	5198.8	11370.2	9887.2
May - Jun	6294.8	25473.3	33448.5	17289.2
Jul - Aug	-	22783.8	14086.5	48310.7
Sep - Oct	14493.9	39336.3	9717.8	13922.2
Nov - Dec	19212.3	26938.8	11983.4	12563.8
Euphausiids				
Jan - Feb	2052.2	1276.6	800.4	334.2
Mar - Apr	4009.8	8424.2	13991.4	24019.8
May - Jun	4347.9	5128.1	4984.4	24726.6
Jul - Aug	-	5722.6	5928.9	8204.9
Sep - Oct	1718.3	4088.6	2625.4	5671.0
Nov - Dec	3135.9	7751.4	2773.6	2251.2
Mysids				
Jan - Feb	131.5	101.9	265.3	12.2
Mar - Apr	60.4	65.1	152.5	5.0
May - Jun	0.0	0.0	907.4	62.8
Jul - Aug	-	118.9	839.0	45.6
Sep - Oct	752.4	371.7	5814.2	12.3
Nov - Dec	170.4	545.7	4466.0	90.6
Decapoda				
Jan - Feb	6381.2	240.2	219.9	50.0
Mar - Apr	309.7	804.6	2903.6	190.2
May - Jun	9237.0	7767.5	15529.2	1551.3
Jul - Aug	-	3461.8	7562.5	2712.4
Sep - Oct	13269.6	1949.2	4336.6	726.4
Nov - Dec	5965.4	882.0	650.9	2582.6
Avg. of all Crustacean Micronekton	4938.3	7249.5	6551.2	7443.1
Avg. Biomass (mg)	5926.0	8699.3	7861.4	8931.8
Avg. DW Biomass (g/10m ²)	5.93	8.70	7.86	8.93
WW g/10 m ²	55.11	80.90	73.11	83.07
Chaetognaths				
Dry Weight (mg/10m ²)				
Jan - Feb	122.8	91.5	39.8	14.7
Mar - Apr	75.1	85.9	132.5	7.8
May - Jun	234.8	315.1	440.5	36.1
Jul - Aug	-	479.4	449.8	25.8
Sep - Oct	585.4	408.7	258.8	80.3
Nov - Dec	549.1	488.0	168.5	84.08
Avg. Chaetognath DW (mg)	313.5	311.4	248.3	41.5
Avg. WW (dw/0.082)	3776.8	3752.0	2991.7	499.6
WW g/10 m ²	3.8	3.8	3.0	0.5

8. Macrobenthos (polychaetes, crustaceans, mollusks, other)

Joseph J. Vitaliano, Steven A. Fromm, and Vincent G. Guida (nodes #9-12)

Background

Macrobenthos are defined as invertebrates living in or on the sediments that are quantitatively sampled by a 0.1 m² Smith McIntyre grab and are retained on a 1.0 mm or 0.5 mm sieve. In the NEFSC, a 1.0 mm sieve was used until the middle of 1979 and a 0.5 mm sieve was used thereafter. Wet weight biomasses were determined for each species in a sample by blot-drying the species collections on absorbent paper towels for about three minutes and weighing them to the nearest mg (Holme and McIntyre 1984). Wet weight biomasses include the shell in molluscs, the carapaces in crustaceans, and the tests in echinoderms. For EMAX, the macrobenthos were separated into four major taxonomic groups (polychaetes, crustaceans, molluscs, and other) that will occupy separate network compartments. The macrobenthos group “other” contains the echinoderms, nemerteans, tunicates, and coelenterates.

The specific feeding mechanisms for many benthic invertebrates in nature are uncertain. For example, polychaetes with well-developed jaws and eyes were found in field surveys to have their fecal matter packed with algal cells and enzymes in their gut capable of digesting cellulose (Warwick *et al.* 1979). Many spionid polychaetes are surface deposit feeders under low flow conditions but switch to filter feeding under high flow conditions (Dauer *et al.* 1981). In general, the polychaetes on the Northeast U.S. Continental Shelf Ecosystem are deposit feeders, filter feeders, omnivores and carnivores. The bivalve molluscs such as *Arctica islandica*, *Spisula solidissima*, and *Pitar morrhuanus* are filter feeders but the bivalves *Nucula proxima* and *Tellina agilis* are deposit feeders. Gastropod molluscs are generally carnivores and scavengers. The crustaceans are carnivores, scavengers, deposit feeders, filter feeders and omnivores. The nemerteans are generally carnivores, while the tunicates are filter feeders. Although the coelenterates are mostly carnivores, the smaller Cerianthids (a dominant coelenterate in our collections) are considered suspension feeders on live and dead material. Sand dollars are a dominant echinoderm in the NEUS Ecosystem and are deposit and suspension feeders. The sea cucumber, *Molpadia oolitica*, is locally abundant in the GOM and is a deposit feeder. Brittle stars are particle feeders and sea stars are carnivores (Caracciolo and Steimle 1983).

Species Lists

Over 2,000 benthic invertebrate species have been identified in the NEFSC surveys in the NEUS Ecosystem and their individual biomasses have contributed to the total biomass of the taxonomic groups in the four EMAX regions. The species listed in Table 8.1 include the 10 dominant taxa in terms of total biomass from each of the taxonomic groups in each geographic region.

Data Sources

Since no benthic data were available for the EMAX regions between 1996 and 2000, we used historical data contained in the Oracle table BENCAT (Benthic Survey Catch database, NEFSC) to estimate biomass for the four macrobenthos taxonomic groups in the EMAX regions. BENCAT includes grab data from a number of surveys conducted by the NEFSC in the NEUS coastal and shelf waters over the past 40 years. These included Wigley and Theroux benthic

sampling between 1956 – 1964; Ocean Pulse and Northeast Monitoring Program 1979-1985; and the 12 Mile Dump Site Study 1986-1989 (Wigley and Theroux 1981; Steimle 1990; Reid *et al.* 1991; Theroux and Wigley, 1998).

Quantitative Approach for Biomass Estimates

The total wet weight biomass for each taxonomic group (polychaetes, crustaceans, molluscs, and others) within a grab sample was summed for all grab samples within a specific geographic region (GOM, GB, SNE and MAB) over all years. This value was divided by the total number of grab samples taken within the specific geographic region over all years. Only those grabs where biomass data were available were used to calculate this total. This result is an estimate of the average wet weight biomass in $\text{g } 0.1 \text{ m}^{-2}$ for the specific taxonomic group in the specific geographic region over all years. This value was multiplied by 10 to extrapolate the estimate from the area of the grab (0.1 m^{-2}) to a square meter.

Example Results

The biomass estimates for the taxonomic groups in each of the EMAX regions (Figure 8.1) are comparable to previously published biomass estimates for the same regions, e.g., Wigley and Theroux benthic sampling between 1956 – 1964 (Wigley and Theroux 1981; Theroux and Wigley 1998) and Ocean Pulse (Steimle 1990).

The biomass estimates for macrobenthos on the NEUS Continental Shelf Ecosystem (Figure 8.1) are subject to a number of possible errors. There were differences among the four geographic regions in the total number of data points (grab samples) that were used to estimate biomass values for the entire geographic region. The total number of Smith McIntyre grab samples taken from each of the geographic regions break down as follows: GOM = 330, GB = 344, SNE = 1,648, and MAB = 487. There were also differences in the temporal and spatial distribution of the grab samples within each of the geographic regions. It is well known that the abundances and biomasses of individual marine benthic invertebrate species can be highly variable in both time and space. Thus it cannot be certain if the biomass values (Figure 8.1) are an accurate estimate of the biomasses for the entire geographic region or are representative of the biomasses for the four taxonomic groups between 1996 and 2000 (the time period being modeled in EMAX). However, Steimle (1990) suggests a long-term stability in overall biomass on the NEUS Ecosystem based on data from the Ocean Pulse surveys. Another source of error was the use of different sieve sizes to process the samples in the various surveys. Theroux and Wigley (1998) used a 1.0 mm sieve and Reid *et al.* (1991) used a 0.5 mm sieve. The Ocean Pulse monitoring surveys (Steimle 1990) used a 1.0 mm sieve from 1978 until the first half of 1979 and a 0.5 mm sieve thereafter. Steimle (1990) compared the retention efficiency between the 1.0 mm and 0.5 mm sieves. On average, the 0.5 mm sieve retained only 4% greater biomass than the 1.0 mm sieve. Since this difference is low, no adjustments were made to the biomass estimates.

A number of other possible errors were identified in the macrobenthos biomass estimates. For a number of invertebrate species on the NEUS Ecosystem, there was overlap in the biomass data between the macrobenthos, sampled by Smith McIntyre grab, and the megabenthos, sampled by scallop dredge, otter trawl, and the Campbell grab. Since the Smith McIntyre grab does not quantitatively sample larger mobile invertebrates very well, we made the following adjustments to the macrobenthos biomass estimates to eliminate this overlap. The biomasses for

decapod crabs were subtracted out of the biomass estimate for macrobenthos - crustaceans, the biomasses of *Arctica islandica* and *Spisula solidissima* were subtracted out of the biomass estimate for macrobenthos - molluscs, and the biomasses for the asteroids (starfish) were subtracted out of the biomass estimate for macrobenthos - other. The biomass data for all these taxa will be included in the megabenthos compartments. In another situation, the total biomass for an unknown bivalve species in one grab sample from the MAB was 0.5 the total biomass for all molluscs in all 487 grab samples in that region. This one grab contained 12,000 bivalve individuals with a biomass of 3,242 grams. It is unknown if these data are real or if there is a data entry error. Since the data from this one grab collected from the offshore waters near the Chesapeake Bay would have heavily influenced the biomass estimate for molluscs over the entire MAB region, we decided to eliminate the data from this grab in the biomass calculation.

Method for Estimating Annual Macrobenthos Production

A number of studies (Wildish 1984; Collie 1985; Steimle 1989; Steimle *et al.* 1990; Maurer *et al.* 1992; Seitz and Schaffner 1995; Sarda *et al.* 2000) have directly measured the production of benthic invertebrate species populations along the NEUS coast. Of these studies, Collie (1985); Steimle (1989); and Steimle *et al.* (1990) have measured production in the open waters of the NEUS Ecosystem within the EMAX geographic regions. The species for which production estimates have been made represent a small fraction of the important species in terms of biomass in the four EMAX geographic regions (see Table 8.1). Direct production measurements are costly and labor intensive.

Since production data are not available even for the most common species of the NEUS Ecosystem, the general relationship between production and biomass, the P:B ratio, was used to estimate production for each of the taxonomic groups (polychaetes, crustaceans, molluscs, and others) in each of the geographic regions. To help with the decision regarding the best P:B ratios to use for the EMAX network, we relied extensively on Steimle (1985; 1987), the studies listed in the first paragraph, and Brey (1990), Cartes *et al.* (2002), Steimle *et al.* (2002) and others. Steimle (1985; 1987) determined the most appropriate P:B ratios to use for a number of taxonomic groups on Georges Bank and the NY Bight based on published P:B ratios from the direct production studies of species from the NEUS Ecosystem and on production studies of similar species at similar latitudes from around the world. The specific P:B ratios used to calculate production for the macrobenthos compartments in the EMAX network (Table 8.2) were determined based on the dominant species in each taxonomic group within each geographic region (Table 8.1).

The use of P:B ratios to estimate production is subject to a number of general errors as well as errors specific to its use in the EMAX network. The production of a given invertebrate population at a given site is dependent on the annual temperature regime, the quality and quantity of food influx, the size of the individuals in the population, life span, and most likely other environmental and biological variables. The P:B ratio does not account for these variables (Steimle 1990; Brey *et al.*, 1996; and Sarda 2000). In the EMAX network, the P:B ratio is applied to all species in a given taxonomic group and all habitats within a wide geographic region to estimate production over that entire region.

Consumption

Background

Consumption rates have been measured for only a few benthic invertebrate species, and most measurements have been conducted under laboratory conditions and for filter feeding bivalves. There are no measurements of consumption rates for the benthic invertebrates in the four EMAX regions. Both Valiela (1995) and Dame (1996) estimated ecological efficiency (P:C) at approximately 10% based on literature values for invertebrates and bivalves, respectively.

Quantitative Approach for Estimates

We used $P:C = 0.10$ to estimate consumption from our production estimates for the macrobenthos nodes in the four EMAX regions. These are crude estimates since consumption rates for benthic invertebrates in the field are dependant on temperature, size, age, and food supply (Valiela, 1995; Velasco and Navarro, 2005).

Example Results

Table 8.3 shows the estimates for production and consumption of the macrobenthos nodes. Production was calculated from the biomass estimates (Figure 8.1) and the derived P:B ratios (Table 8.2). Consumption was calculated using the production estimates for each macrobenthos node and an assumed ecological efficiency of 10 percent.

Macrobenthos (polychaetes, crustaceans, molluscs, other) respiration estimates

Background

There is considerable literature on respiration rates among benthos. Most published work falls into two basic categories: benthic system respiration (e.g., Hopkinson *et al.* 2001) and respiration of selected benthic animal species (e.g., Emerson *et al.* 1988). Neither of these categories provided data directly applicable to the current study. Most benthic system studies do not treat functional grouping (like our nodes) separately, and data on such factors as size distributions, feeding status, activity level, and life history stage and temperature responses are inadequately known for all but a few of the nearly 2,000 benthic species of the NEUS Ecosystem (Theroux and Wigley 1998). One study in which system respiration was built up from individual species data and partitioned into functional groupings (Piepenberg *et al.* 1995) is from an arctic system whose species composition, temperature and depth regimes are so different from ours that comparison is questionable.

Quantitative Approach for Respiration Estimates

For the reasons described above, we chose to estimate respiration values for the macrobenthic nodes from other composite parameters for the same groups:

$$(EQ. 8.1) \quad R = C \times E_A \times 0.65,$$

Where R is respiration, C is consumption, E_A is assimilation efficiency, and 0.65 represents the fraction of assimilated energy that is typically respired by ectotherms (Parry 1983). Values for assimilation efficiencies for this purpose were derived from Valiela (1995).

Example Results

Table 8.4 shows the estimates for respiration of the macrobenthos nodes. Respiration was calculated using Equation 8.1 and the specific assimilation efficiency.

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Table 8.1. Dominant benthic taxa in biomass for the EMAX regions.

TAXONOMIC GROUP	GOM	GB	SNE	MAB
CRUSTACEANS	<i>Amphipoda</i> unident. <i>Pagurus pubescens</i> <i>Leptocheirus pinguis</i> <i>Politolana impressa</i> <i>Meganyctiphanes</i> sp. <i>Pandalus propinquus</i> <i>Isopoda</i> unident. <i>Politolana polita</i> <i>Unciola</i> sp. <i>Cirolana</i> sp.	<i>Amphipoda</i> unident. <i>Corophium crassicorne</i> <i>Ampelisca agassizi</i> <i>Leptocheirus pinguis</i> <i>Pagurus</i> sp. <i>Byblis serrata</i> <i>Diastylis quadrispinosa</i> <i>Unciola irrorata</i> <i>Unciola</i> sp. <i>Unciola inermis</i>	<i>Amphipoda</i> unident. <i>Ampelisca agassizi</i> <i>Leptocheirus pinguis</i> <i>Unciola inermis</i> <i>Unciola irrorata</i> <i>Gammarus annulatus</i> <i>Cirolana polita</i> <i>Byblis serrata</i> <i>Edotea acuta</i> <i>Crangon septemspinosa</i>	<i>Ampelisca agassizi</i> <i>Pagurus pollicaris</i> <i>Unciola irrorata</i> <i>Rhepoxynius hudsoni</i> <i>Pagurus acadianus</i> <i>Ampelisca vadorum</i> <i>Unciola inermis</i> <i>Pagurus longicarpus</i> <i>Crangon septemspinosa</i> <i>Pseudunciola obliqua</i>
POLYCHAETES	<i>Spio filicornis</i> <i>Polychaeta</i> unident. <i>Nephtys incisa</i> <i>Sternaspis fossor</i> <i>Nephtys</i> sp. <i>Maldane sarsi</i> <i>Onuphis opalina</i> <i>Anobothrus gracilis</i> <i>Lumbrineris</i> sp. <i>Aphrodita</i> sp.	<i>Filograna implexa</i> <i>Polychaeta</i> unident. <i>Nephtys</i> sp. <i>Sternaspis scutata</i> <i>Ninoe nigripes</i> <i>Aglaophamus circinata</i> <i>Scalibregma inflatum</i> <i>Lumbrineris magalhaensis</i> <i>Nephtys bucera</i> <i>Spiophanes bombyx</i>	<i>Pherusa affinis</i> <i>Nephtys incisa</i> <i>Polychaeta</i> unident. <i>Streblosoma</i> sp. <i>Lumbrineris acicularum</i> <i>Ninoe nigripes</i> <i>Spio setosa</i> <i>Capitellidae</i> <i>Spiophanes bombyx</i> <i>Glycera dibranchiata</i>	<i>Polychaeta</i> unident. <i>Lumbrineris acicularum</i> <i>Glycera dibranchiata</i> <i>Spiophanes bombyx</i> <i>Chone infundibuliformis</i> <i>Lumbrineris hebes</i> <i>Asabellides oculata</i> <i>Ampharete arctica</i> <i>Nephtys picta</i> <i>Aphrodita hastata</i>
MOLLUSCS - BIVALVES	<i>Cyclocardia borealis</i> <i>Astarte crenata</i> <i>Mytilus edulis</i> <i>Bivalvia</i> unident. <i>Nucula</i> sp.	<i>Bivalvia</i> unident. <i>Cyclocardia borealis</i> <i>Astarte undata</i> <i>Modiolus modiolus</i> <i>Anomia aculeata</i>	<i>Pitar morrhuanus</i> <i>Nucula proxima</i> <i>Bivalvia</i> unident. <i>Astarte undata</i> <i>Modiolus modiolus</i>	<i>Nucula proxima</i> <i>Mytilus edulis</i> <i>Cyclocardia borealis</i> <i>Ensis directus</i> <i>Astarte undata</i>

Table 8.1, continued.

TAXONOMIC GROUP	GOM	GB	SNE	MAB
MOLLUSCS - GASTROPODS	<i>Colus stimpsoni</i> <i>Aporrhais occidentalis</i> <i>Colus pubescens</i> <i>Colus pygmaeus</i> <i>Buccinum undatum</i>	Gastropoda unident. <i>Buccinum undatum</i> <i>Euspira heros</i> <i>Lunatia triseriata</i> <i>Pleurobranchaea</i> sp.	<i>Nassarius trivittatus</i> <i>Buccinum</i> sp. <i>Busycon canaliculatum</i> <i>Colus pygmaeus</i> Gastropoda unident.	<i>Nassarius trivittatus</i> <i>Buccinum undatum</i> <i>Neverita duplicata</i> Gastropoda unident. <i>Pleurobranchaea tarda</i>
OTHERS - NEMERTEANS	Rhynchocoela	Rhynchocoela	Rhynchocoela	Rhynchocoela
OTHERS - ECHINODERMS	<i>Molpadia oolitica</i> <i>Echinarachnius parma</i> <i>Brisaster fragilis</i> <i>Ophiura sarsi</i> <i>Schizaster</i> sp.	<i>Echinarachnius parma</i> <i>Ophiura sarsi</i> <i>Arbacia punctulata</i> <i>Steroderma unisemita</i> <i>Strongylocentrotus droebachiensis</i>	<i>Echinarachnius parma</i> <i>Havelockia scabra</i> <i>Molpadia oolitica</i> <i>Amphioplus abditus</i> Ophiuroidea unident.	<i>Echinarachnius parma</i> <i>Sclerodactyla briareus</i> <i>Encope emarginata</i> <i>Mellita quinquiesperforata</i> Cucumariidae unident.
OTHERS - COELENTERATES	<i>Cerianthus</i> sp. <i>Actinauge verrilli</i> <i>Pennatula aculeata</i>	<i>Cerianthus</i> sp. Hydrozoa <i>Ceriantheopsis americanus</i>	<i>Ceriantheopsis americanus</i> <i>Cerianthus</i> sp. <i>Edwardsia elegans</i>	<i>Ceriantheopsis americanus</i> Actiniaria unident. <i>Paranthus rapiformis</i>
OTHERS - TUNICATES	Ascidacea	<i>Molgula arenata</i>	Ascidacea	Ascidacea

Table 8.2. P:B ratios used to estimate production for the macrobenthos compartments in the EMAX network.

	GOM	GB	SNE	MAE
Polychaetes	2.5	2.5	2.5	2.5
Crustacea	3.0	3.0	3.0	3.0
Molluscs	2.0	2.0	2.0	2.0
Other	2.0	2.0	2.0	2.0

Table 8.3. Production and consumption values for macrobenthos.

Region	Taxonomic Group	Production g/m ² /yr wet wt.	Consumption g/m ² /yr wet wt.
GOM	Macrobenthos - POLYCHAETES	33.7290	337.2902
GOM	Macrobenthos - CRUSTACEANS	5.5049	55.0491
GOM	Macrobenthos - MOLLUSCS	37.7935	377.9352
GOM	Macrobenthos - OTHERS	144.7836	1447.8364
GB	Macrobenthos - POLYCHAETES	12.9177	129.1766
GB	Macrobenthos - CRUSTACEANS	49.3944	493.9439
GB	Macrobenthos - MOLLUSCS	21.6856	216.8564
GB	Macrobenthos - OTHERS	163.3574	1633.5744
SNE	Macrobenthos - POLYCHAETES	88.5906	885.9059
SNE	Macrobenthos - CRUSTACEANS	18.4225	184.2251
SNE	Macrobenthos - MOLLUSCS	86.3779	863.7791
SNE	Macrobenthos - OTHERS	78.0826	780.8258
MAB	Macrobenthos - POLYCHAETES	30.9974	309.9743
MAB	Macrobenthos - CRUSTACEANS	9.8666	98.6661
MAB	Macrobenthos - MOLLUSCS	131.1182	1311.1815
MAB	Macrobenthos - OTHERS	189.0246	1890.2460

¹ Assuming a 10 per cent ecological efficiency

Table 8.4. Respiration values for macrobenthos.

Region	Taxonomic Group	Consumption g m^{-2} yr^{-1} wet wt.	Assimilation Efficiency	Respiration g m^{-2} yr^{-1} wet wt.
GOM	Macrobenthos - POLYCHAETES	337.2909	0.5	109.6195
GOM	Macrobenthos - CRUSTACEANS	55.0491	0.5	17.8910
GOM	Macrobenthos - MOLLUSCS	377.9352	0.4	98.2632
GOM	Macrobenthos - OTHER	1447.8364	0.5	470.5468
GB	Macrobenthos - POLYCHAETES	129.1766	0.5	41.9824
GB	Macrobenthos - CRUSTACEANS	493.9439	0.5	160.5318
GB	Macrobenthos - MOLLUSCS	216.8564	0.4	56.3827
GB	Macrobenthos - OTHER	1633.5744	0.5	530.9117
SNE	Macrobenthos - POLYCHAETES	885.9059	0.5	287.9194
SNE	Macrobenthos - CRUSTACEANS	184.2251	0.5	59.8732
SNE	Macrobenthos - MOLLUSCS	863.7791	0.4	224.5826
SNE	Macrobenthos - OTHER	780.8258	0.5	253.7684
MAB	Macrobenthos - POLYCHAETES	309.9743	0.5	100.7416
MAB	Macrobenthos - CRUSTACEANS	98.6661	0.5	32.0665
MAB	Macrobenthos - MOLLUSCS	1311.1815	0.4	340.9072
MAB	Macrobenthos - OTHER	1890.2460	0.5	614.3300

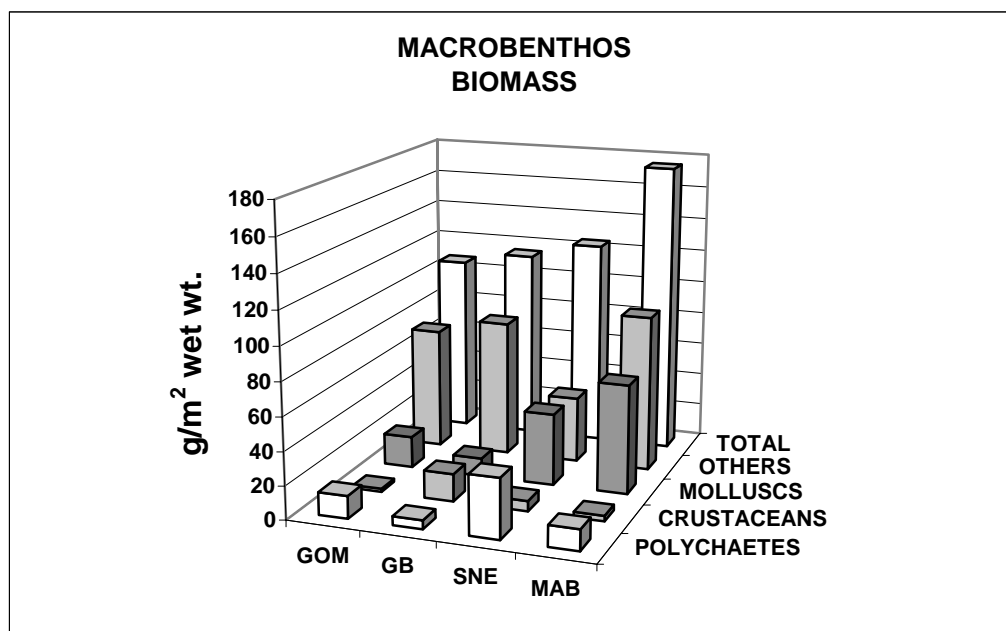


Figure 8.1. Biomass estimates in grams per square meter wet weight for the taxonomic groups in the four EMAX regions.

9. Megabenthos - Filterers

William T. Stockhausen and Vincent G. Guida (node #13)

Background

Although not strictly defined in terms of size, the largest benthic invertebrates are often referred to as “megabenthos”. For the purposes of this modeling exercise, we defined megabenthos filter feeders to include three species of large, commercially exploited bivalves: ocean quahog, *Arctica islandica*; Atlantic surf clam, *Spisula solidissima*; and sea scallop, *Placopecten magellanicus*. Other kinds of bivalves, including mussels (e.g., *Mytilus edulis* and *Modiolus modiolus*), numerous species of small clams, cockles, jingle shells, and others are included in the macrobenthos (polychaetes, crustaceans, mollusks, and others) node (Section 8 of this document).

The ocean quahog is a large, temperate to boreal, infaunal clam with an amphi-Atlantic distribution (Weinberg 1995). It is widely distributed across the continental shelf in medium- to fine-grained sand from the Delmarva Peninsula to Georges Bank (Cargnelli *et al.* 1999a), including nearshore waters in the Gulf of Maine (Wigley and Theroux 1998). It has low recruitment and slow growth rates (Kennish *et al.* 1994; Kennish and Lutz 1995). The Atlantic surf clam is another large infaunal clam found in fine sand to gravel, ranging from the Gulf of St. Lawrence to Cape Hatteras (Merrill and Ropes 1969; Cargnelli *et al.* 1999b). The sea scallop is an epifaunal bivalve living in coarse gravelly or shelly sand to gravel and rock, whose range is similar to that of the surf clam. Sea scallops are moderately abundant only in nearshore waters in the Gulf of Maine (Packer *et al.* 1999).

Data Sources

Fisheries independent survey data from the NEFSC Clam and Scallop Surveys were used to estimate biomass density (g meat weight m^{-2}). The surveys do not sample in the Gulf of Maine (GOM) since biomass densities are low for the three species of bivalves in this node outside state waters in this region. Therefore, data for the GOM subregion was derived from grab sample values (Theroux and Wigley 1998).

Quantitative Approach for Biomass Estimates

Ocean Quahogs and Atlantic Surfclams

Survey data from the NEFSC Clam Surveys for 1997 and 1999 were used to estimate biomass densities of ocean quahogs and Atlantic surfclams in each EMAX region. For each tow, reported shell lengths were converted to meat weights using species- and region-specific length-meat weight regressions (Table 9.1; NEFSC 2003, 2004). Total meat weight caught in a tow was calculated by summing over the individual weights for each species. Area-stratified mean catch per tow was then calculated for each EMAX region and species combination using the total meat weights from stations in survey strata contained within the EMAX region. Efficiency-corrected estimates of species biomass density in EMAX region r and survey year y , d_{ry} (g meat weight m^{-2}), were calculated from the corresponding area-stratified mean catch per tow, c_{ry} , using the formula

$$(EQ. 9.1) \quad d_{ry} = \frac{A_s}{A_r} \frac{d_s}{\bar{d}} \frac{c_{ry}}{a_s \varepsilon}$$

where A_r is the area corresponding to EMAX region r ; A_s is the area of the sampled survey strata within the EMAX region; d_s is the standard tow distance; \bar{d} is the average tow distance; a_s is the area swept during a standard tow; and ε represents the efficiency of the gear (Table 9.2).

The last ratio in Equation 9.1 is the typical expansion of catch per tow to efficiency-corrected biomass density. The first two terms apply corrections for differences between (1) the sampled survey area and the EMAX region, and (2) distances of a “standard” tow and an average tow. Although strata covering the entire continental shelf are defined for the surveys, typically not all strata are sampled during a survey. Strata where clams are known (or assumed) to be absent are not sampled by the survey. Consequently, survey-based estimates of biomass density will be higher than appropriate for an EMAX region (Tables 9.3 and 9.4). The factor A_s/A_r corrects for this inflation by scaling the biomass density derived from sampled survey strata to an entire EMAX region. Similarly, the factor of d_s/\bar{d} corrects for relative bias due to differences in tow distance between a “standard” tow (upon which area swept, a_s , is based) and an average tow.

Finally, estimates of average biomass density for each EMAX region, d_r , were obtained by averaging the d_{ry} over the individual surveys.

Sea Scallops

Survey data from the NEFSC Scallop Surveys for 1996-2000 were used to estimate biomass densities of sea scallops in each EMAX region. For each tow, reported shell heights were converted to meat weights using region-specific length-meat weight regressions (Table 9.5; NEFSC 2001). In addition, a length-specific correction for gear selectivity between lined and unlined scallop dredges was included prior to calculating total meat weight. Total meat weight (in grams) caught for a given tow was calculated by summing over the individual selectivity-adjusted meat weights, as in

$$(EQ. 9.2) \quad W = \sum_i \left[\frac{0.7148 e^{0.9180 - 0.7148 \cdot ((160 - L_i) - 106.3091)} + e^{0.9180 \cdot ((160 - L_i) - 106.3091)}}{e^{0.9180 - 0.7148 \cdot ((160 - L_i) - 106.3091)} + e^{0.9180 \cdot ((160 - L_i) - 106.3091)}} \right]^{-1} (e^{\alpha} L_i^{\beta})$$

where L_i is the shell height (in mm) of the i th scallop, and α and β are coefficients of the region-specific length-meat weight regression equation. The term in brackets represents the adjustment for the selectivity of the lined survey dredge, while the term in parentheses converts shell height to meat weight (in grams). Only scallops with shell heights > 40 mm were included in this calculation.

The remaining calculations were similar to those used for ocean quahogs and Atlantic surfclams. Parameters used to calculate d_{ry} for sea scallops are given in Table 9.2.

Example Results

Figure 9.1 shows values for biomass density estimates for the megabenthos - filterers species, sorted by EMAX region.

Production/Growth/Reproduction

No published data were available for any of the three target species. Production values for this node were therefore based on the use of a P:B ratio of 0.8. This value is well within the published range for bivalves (0.28 to 2.91; based on compilation of preexisting data by Dame 1996), and is below the median value, reflecting the slow growth rate of the dominant ocean quahog. No published data was available for any of the three target species.

Consumption

Here again, no published consumption data were available for the target species. Values were based on the use of a C:B ratio of 10. This value is well within values calculated from the compilation of Dame (1.9 to 54.3; 1996), and approaches the value for the American oyster (9.48; Dame 1976).

Respiration

We have chosen to estimate respiration values for the megabenthic nodes from other composite parameters for the same groups:

$$(EQ. 9.3) \quad R = C \times E_A \times 0.65,$$

where R is respiration, C is consumption, E_A is assimilation efficiency, and 0.65 represents the fraction of assimilated energy that is typically respired by ectotherms (Parry 1983). Values for assimilation efficiencies for this purpose were derived from Valiela (1995).

Example Results

Table 9.6 shows values for biomass density, production, consumption, and respiration for megabenthos - filterers in each of the four ecoregions.

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Table 9.1. Shell length-to-meat weight conversion coefficients for ocean quahogs (NEFSC 2004) and Atlantic surfclams (NEFSC 2003). $W = e^{\alpha} L^{\beta}$, where L is in mm and W is in g. SVA-NC = southern Virginia and North Carolina; DMV = Delmarva Peninsula; N/SNJ = northern/southern New Jersey; LI = Long Island; SNE = southern New England; GBK = Georges Bank.

Survey region	Ocean Quahog		Atlantic Surfclam	
	α	β	α	β
SVA-NC	-9.04231	2.787987	-7.0583	2.3033
DMV	-9.04231	2.787987	-9.48913	2.860176
NNJ	-9.84718	2.94954	-9.3121	2.863716
SNJ	-9.84718	2.94954	-9.3121	2.863716
LI	-9.23365	2.822474	-7.9837	2.5802
SNE	-9.12428	2.774989	-7.9837	2.5802
GBK	-8.96907	2.767282	-8.27443	2.654215

Table 9.2. Values of various factors used to convert mean catch per tow to biomass density for ocean quahogs, Atlantic surfclams, and sea scallops.

Factor	Ocean Quahog	Atlantic Surfclam	Sea Scallop
d_s (nm)	0.15	0.15	1.0
\bar{d} (nm)	0.24	0.24	1.0
a_s (nm ²)	0.0008225-0.15	0.0008225-0.15	0.001317-1.0
ε	0.269 (NEFSC 2004)	0.37 (NEFSC 2003)	1.0

Table 9.3. Correspondence between EMAX regions and clam and scallop survey strata. Area corresponds to EMAX region. Three digit scallop strata on GB were defined by splitting strata 62, 63, 65, and 66.

EMAX Region	Clam Strata	Scallop Strata	Area (km ²)
GB	49-74	49-61, 64, 67-74, 621, 622, 631, 632, 651, 652, 661, 662	43,666
GOM	NA	NA	79,128
SNE	25-48, 90-96	25-48, 90-96	64,060
MAB	01-24, 80-89	01-24, 80-89	59,807

Table 9.4. Clam survey regions and defining strata. SVA-NC = southern Virginia and North Carolina; DMV = Delmarva Peninsula; N/SNJ = northern/southern New Jersey; LI = Long Island; SNE = southern New England; GBK = Georges Bank.

Clam Survey Region	Ocean Quahog	Atlantic Surfclam
SVA-NC	5,6	1, 2, 5, 6 80, 81
DMV	9-11, 13-15	9, 10, 13, 14, 82-86
SNJ	17-19, 87	17, 87
NNJ	21-23, 25-27, 88-90	21, 25-28, 88-90
LI	29-31, 33-35, 91-93	29, 30, 33, 34, 91-93
SNE	37-39, 41, 45-47, 94-96	37, 38, 41, 45-47, 94-96
GBK	54-62, 65-74	54, 55, 57, 59, 61, 65, 67-74

Table 9.5. Shell length-to-meat weight conversion coefficients for sea scallops (NEFSC 2001). $W = e^{\alpha} L^{\beta}$, where L is in mm and W is in g.

Region	Alpha	Beta	Source
GB	-11.6038	3.1221	NEFSC 2001
MAB	-12.2484	3.2641	NEFSC 2001

Table 9.6. Rate values for megabenthos filter feeders.

Subregion	Biomass Density (g m ⁻²)	Production (g m ⁻² yr ⁻¹)	Consumption (g m ⁻² yr ⁻¹)	Respiration (g m ⁻² yr ⁻¹)
GOM	5.520	4.4160	55.2000	10.7640
GB	17.4466	13.9573	174.4658	34.0208
SNE	15.6055	12.4844	156.0548	30.4307
MAB	15.4301	12.3441	154.3014	30.0888

Megabenthos--Filter Feeders

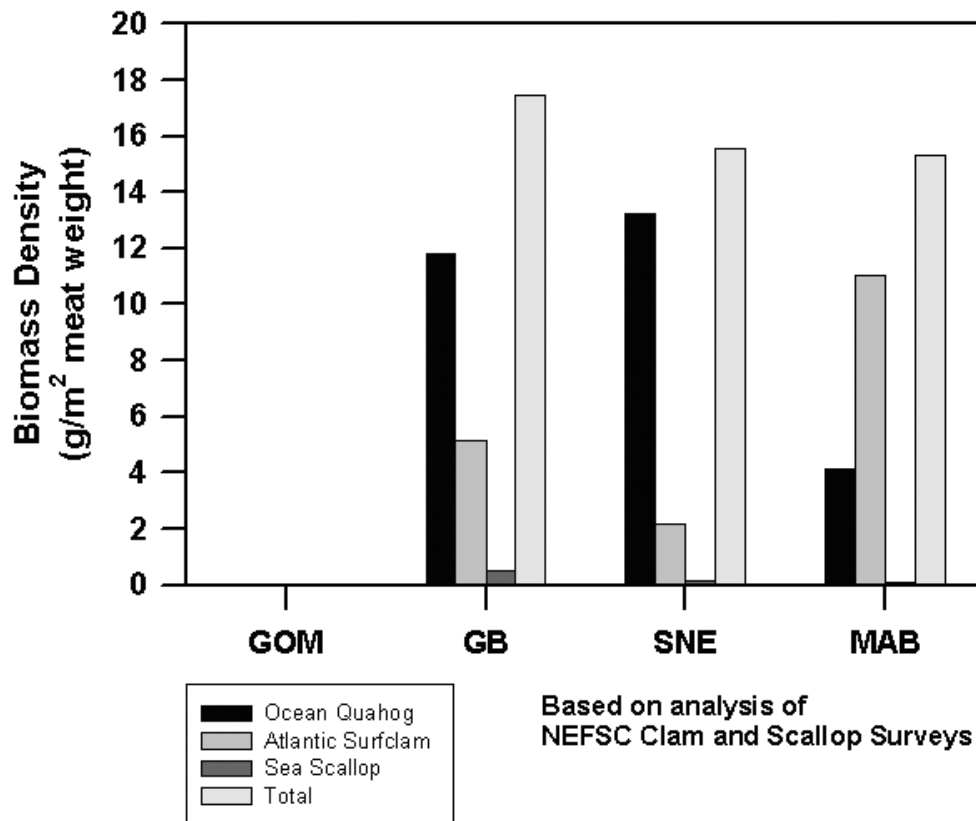


Figure 9.1. Biomass density estimates for the megabenthos - filter feeders species, sorted by EMAX region.

10. Megabenthos - Other

William T. Stockhausen and Vincent G. Guida (node #14)

Background

Although not strictly defined in terms of size, the largest benthic invertebrates are often referred to as “megabenthos”. Aside from large filter-feeding bivalves (megabenthos filterers), there are a variety of mostly predators and scavengers that may fit this description. We have chosen to include two groups: large Arthropods and Asteroid Echinoderms. All other large invertebrates, even if of comparable size, have been consigned to macrobenthos (see Section 8 for a list).

Megabenthic species have been assessed by a number of methods: trawls, dredges, grabs, submersible, towed camera sled, and divers (Uzmann *et al.* 1977; Franz *et al.* 1981; Miller 1989; Stehlik *et al.* 1991; Theroux and Wigley 1998). However, no one study has treated all such organisms comprehensively in this region and no one method is suitable for all of them. Therefore, for purposes of biomass quantification, we have divided the megabenthos biomass in this node into two separate elements, defined by the efficiency of various gear types used to collect them: sea stars (Echinodermata: Asteroidea) and large Arthropods. The latter element includes horseshoe crabs (Merostomata), mantis shrimp (Crustacea: Stomatopoda), crabs (Crustacea: Decapoda: Brachyura and Anomura other than hermit crabs) and lobsters (Decapoda: Astacidea).

Twenty-five species of commonly-occurring Asteroids, including sub-tropical, wide ranging, boreal and subarctic-boreal groups, have been identified from NEFSC groundfish survey data (Franz *et al.* 1981). Species listed in Table 10.1 are dominants from among that list. However, comparison of NEFSC Bottom Trawl Survey data with data from bottom video and still photographs and catches with a small-mesh 2 m beam trawl suggest that these Survey Trawl data greatly underestimate sea star (Asteroid) abundance. Asteroid biomass from grab sampling data (Wigley and Theroux 1981, Theroux and Wigley 1998) more closely resembles estimates based on visual assessments and beam trawl catches that ranged from about 0.5 to 5.0 g m⁻² (Guida, unpublished).

Decapod biomasses from these grab sampling sources were substantially larger than from NEFSC Bottom Trawl Survey data, but were not comparable because they were heavily dominated by small Decapods (e.g., crangonid shrimps and hermit crabs), which are included in the macrobenthos (Section 8) in this document. Larger Decapods were admittedly underrepresented in grab samples (Theroux and Wigley 1998). The species list is given in Table 10.1.

Data Sources

Fisheries-independent survey data from the NEFSC Bottom Trawl Survey were used to estimate biomass density (g wet weight m⁻²) for large arthropods. Comparison of NEFSC Bottom Trawl Survey data with data from bottom video and still photographs and catches with a small-mesh 2 m beam trawl net suggest that while these Trawl Survey data provide reasonable estimates for large arthropods, they greatly underestimate Asteroid density (Guida, unpublished). Sea star biomass was derived from comprehensive regional benthic grab data (Wigley and Theroux 1981; Theroux and Wigley 1998).

Quantitative Approach for Biomass Estimates

Large Arthropods

For each species and EMAX region, mean catch per tow (in kg tow^{-1}) was first calculated on a per-survey basis over survey strata contained within the EMAX region (Table 10.2, see also Table 1.1) using both spring and fall surveys during the period 1996-2000. If fewer than two stations were completed in a stratum during a given survey, that stratum was dropped from calculations of mean catch per tow. Mean catch per tow in season s and year y , c_{sy} , was then converted to biomass density (d_{sy}) using the formula

$$(EQ. 10.1) \quad d_{sy} = f \frac{c_{sy}}{a}$$

where a is the area swept by the bottom trawl in a standard tow (0.01 nm^2 for the Bottom Trawl Survey) and f is a conversion factor from kg naut. mi^{-2} to g m^{-2} ($f = [1000 \text{ g/kg}]/[1852 \text{ m/naut. mi}]^2$). Finally, biomass density estimates were averaged over season and year using the formula

$$(EQ. 10.2) \quad d = \frac{1}{5} \sum_y \left\{ \frac{1}{12} \sum_s 6 d_{sy} \right\}$$

where equal weight was given to spring and fall survey results (Figure 10.1).

Except in the Mid-Atlantic Bight, American lobster (*Homarus americanus*) comprised the major component of “other” biomass (Figure 10.1). In the Mid-Atlantic Bight, horseshoe crabs (*Limulus polyphemus*) comprised the major component, with American lobster as the second largest component. The mean lobster value for the four subregions calculated here (0.025 g m^{-2}) closely approximates the 1996 NEFSC autumn bottom trawl survey biomass index for lobster: $1.3 \text{ kg tow}^{-1} = 0.027 \text{ g m}^{-2}$ (Idoine 1996).

Comparative sampling of the same set of stations using 36' Yankee otter trawl (as used in the NEFSC Bottom Trawl Survey), 2 m beam trawl with 6.4 mm (1/4") mesh, and video drift vehicle (Guida, unpublished) indicated that a catchability factor was needed for data on large Arthropods other than the American lobster. Table 10.3 compares catches of *Cancer* spp. crabs (*C. borealis* and *C. irroratus* could not be distinguished in the video images) taken from the same stations during three NEFSC Benthic Habitat cruises conducted near Hudson Canyon (SNE Region). Biomass densities for net catches were calculated by dividing total wet weight by the estimated area swept out by the respective trawl gears. Video biomass densities were calculated by multiplying counts of individuals seen in the video by the mean individual weight as determined from the beam trawl catch and dividing by the area of the video drift transect.

Although not all methods were employed during each cruise, it is clear that 36' Yankee estimates were about two orders of magnitude smaller than densities based on either beam trawl catches or bottom video counts. Assuming the bottom video biomass represents the actual crab density, a catchability of about 50% for the beam trawl and 1% for 36' Yankee for these large Arthropods is suggested by the mean values and by the data from August 2004, when all three methods were employed. Therefore, NEFSC survey values for all large Arthropods other than the American lobster will be multiplied by 100 to obtain realistic estimates.

Unlike *Cancer* spp., the American lobster was too rarely caught in the beam trawl or in video images to be able to assess its biomass density by those means for comparison with 36'

Yankee values. Thus, no unique catchability factor could be assigned. From behavioral observation, it appears that catchability factor for lobsters might be far higher than for *Cancer* spp. crabs because the former, unlike the latter, tends to propel itself off the bottom with “tail thrusts” when disturbed, making otter trawl capture more likely. On the other hand, lobsters are more likely than *Cancer* crabs to be found in rocky areas (Hudon and Lamarche 1989), where capture by mobile gear is not possible. This may be disproportionately true of juveniles (Steneck *et al.* 1991). Choosing to err on the side of conservatism, lobsters have therefore been assigned a catchability of 100%, which probably greatly underestimates their abundance and biomass.

Asteroids

General comments provided for macrobenthos (Section 8) regarding biomass estimates from grab sample data apply to our estimates of the Asteroid element of the megabenthos as well.

Example Results

Figures 10.1 and 10.2 show estimated biomass for megabenthos - other sampled from the two survey methodologies, with a single focus on large arthropods (10.1) and all species combined (10.2).

Production/Growth/Reproduction

Production was estimated using a P:B ratio of 1.5 based on the assumption that as large, active invertebrates, P:B should resemble that of squid and shrimp.

Consumption

Consumption was estimated using a C:B ratio of 13.5 based again on the assumption that shrimp should resemble other large benthic invertebrates. We estimated consumption by multiplying the C:B ratio by biomass for the megabenthos - other node in the four EMAX regions. These are crude estimates since consumption rates for benthic invertebrates in the field are dependant on temperature, size, age, and food supply (Valiela 1995; Velasco and Navarro 2005).

Respiration

We chose to estimate respiration values for the macrobenthic nodes from other composite parameters for the same groups:

$$(EQ. 10.3) \quad R = C \times E_A \times 0.65,$$

where R is respiration, C is consumption, E_A is assimilation efficiency, and 0.65 represents the fraction of assimilated energy that is typically respired by ectotherms (Parry 1983). Values for assimilation efficiencies for this purpose were derived from Valiela (1995).

Example Results

Values for biomass density, production, consumption, and respiration for megabenthos - other in each of the four subregions are summarized in Table 10.4.

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Table 10.1. Species defined as megabenthos - other.

Scientific name	Common Name	NEFSC Species Code
<i>Limulus polyphemus</i>	Horseshoe crab	318
<i>Homarus americanus</i>	American lobster	301
<i>Scyllarides nodifer</i>	Ridged slipper lobster	302
<i>Scyllarides aequinoctialis</i>	Spanish slipper lobster	303
<i>Panulirus argus</i>	Caribbean spiny lobster	304
<i>Geryon fenneri</i>	Golden deepsea crab	308
<i>Geryon affinis</i>	White crab	309
<i>Geryon quinquedens</i>	Red deepsea crab	310
<i>Canceridae</i>	Cancer crabs, unclassified	311
<i>Cancer borealis</i>	Jonah crab	312
<i>Cancer irroratus</i>	Atlantic rock crab	313
<i>Callinectes sapidus</i>	Blue crab	314
<i>Ovalipes sp</i>	Calico crabs, unclassified	315
<i>Majidae</i>	Spider crabs, unclassified	317
<i>Galatheididae</i>	Galatheids, unclassified	319
<i>Portunidae</i>	Swimming crabs, unclassified	320
<i>Ovalipes stephensoni</i>	Coarsehand lady crab	321
<i>Ovalipes ocellatus</i>	Lady crab	322
<i>Stomatopoda</i>	Mantis shrimps, unclassified	323
<i>Lithodes maja</i>	Northern stone crab	324
<i>Chionoecetes opilio</i>	Snow crab	325
<i>Carcinus maenas</i>	Green crab	326
<i>Hepatus epheliticus</i>	Calico box crab	327
<i>Calappa flammea</i>	Flame box crab	328
<i>Calappa sulcata</i>	Yellow box crab	329
<i>Calappidae</i>	Box crabs, unclassified	339
<i>Asterias forbesii</i>	Common sea star	332
<i>Asterias vulgaris</i>	Boreal asterias	333
<i>Astropecten spp.</i>	Margined sea stars	334
<i>Leptasterias sp.</i>	Slender-armed and polar sea stars	332
<i>Solaster sp.</i>	Sun stars	332
<i>Ctenodiscus crispatus</i>	Mud star	332

Table 10.2. EMAX Regions and NEFSC Bottom Trawl Survey strata.

EMAX Region	NEFSC Strata	Area (km ²)
GB	01130-01230, 01250	43,666
GOM	24,26-30,36-40 03570-03900	79,128
SNE	01010-01120; 03010-03140,03450-03560	64,060
MAB	01610-01760; 03150-03440	59,807

Table 10.3. Comparison of biomass density calculated by various methods for *Cancer* spp. crabs from NEFSC Benthic Habitat cruises.

Cruise Month-Year	36 Yankee Biomass Density (g m^{-2})	Beam Trawl Biomass Density (g m^{-2})	Bottom Video Biomass Density (g m^{-2})
Nov-01	0.0066		
Nov-02		0.3128	0.5788
Aug-04	0.0021	0.1302	0.2665
Jan-05		0.1965	
Mean	0.0043	0.2215	0.4227

Table 10.4. Rate values for megabenthos - other.

Subregion	Biomass Density (g m^{-2})	Production ($\text{g m}^{-2} \text{yr}^{-1}$)	Consumption ($\text{g m}^{-2} \text{yr}^{-1}$)	Respiration ($\text{g m}^{-2} \text{yr}^{-1}$)
GOM	1.1256	1.6884	15.1959	6.9142
GB	3.5056	5.2584	47.3259	21.5333
SNE	1.8048	2.7073	24.3654	11.0863
MAB	4.8325	7.2487	65.2385	29.6835

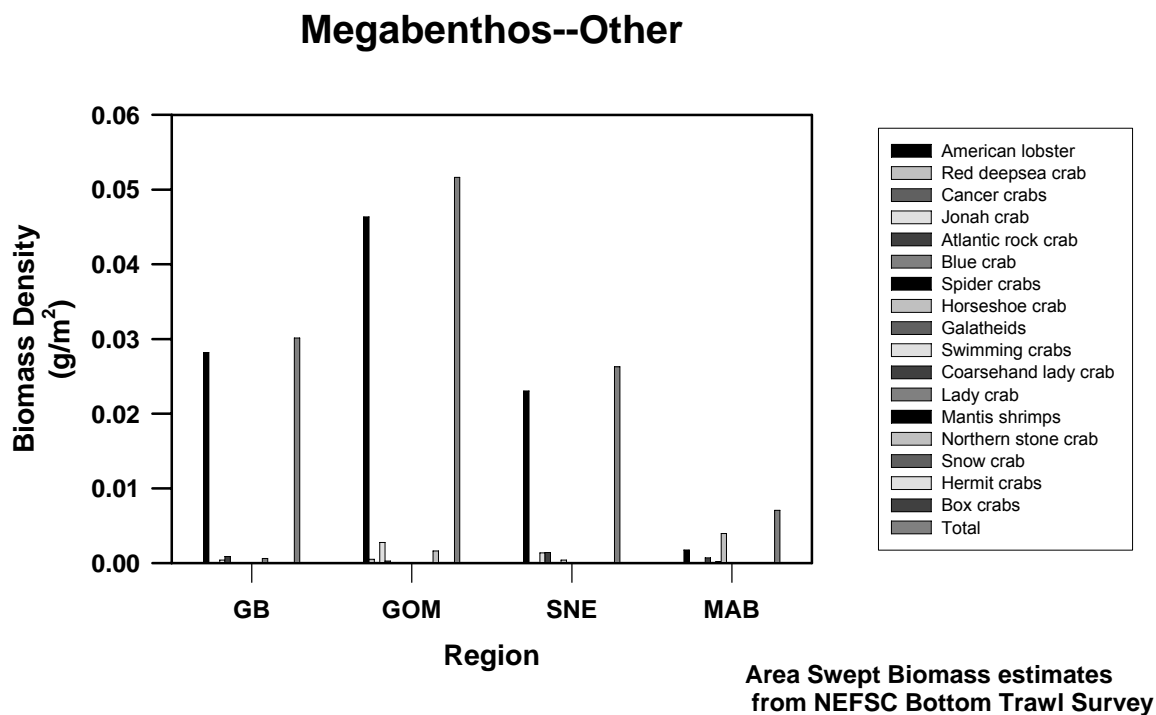


Figure 10.1. Biomass density estimates for the megabenthos - other large arthropod species.

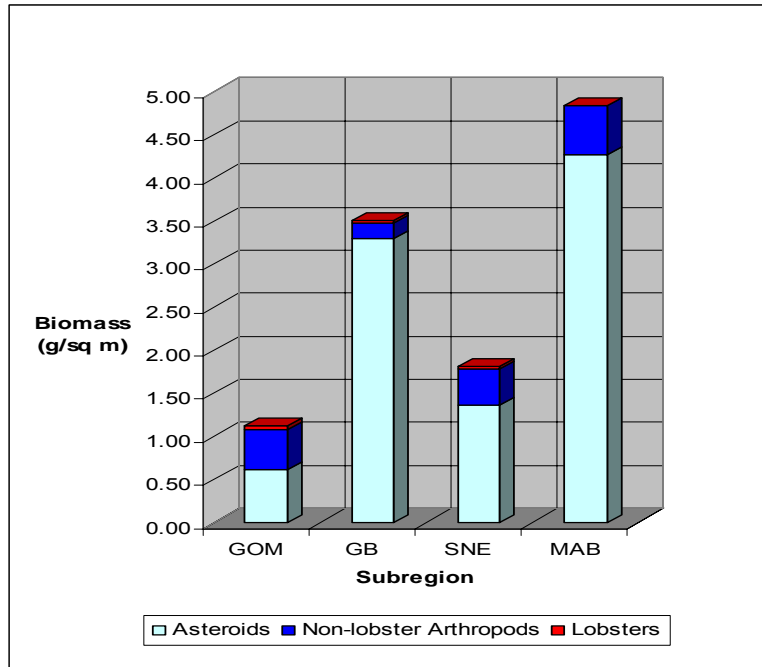


Figure 10.2. Combined biomass density estimates for various elements of the megabenthos - other: Large Non-lobster Arthropods (modified for catchability) from NEFSC Trawl Survey; Lobsters (unmodified) from NEFSC Trawl Survey; and Asteroids from grab sample data (Wigley and Theroux 1981, Theroux and Wigley 1998).

11. Shrimp and Similar Species

Christopher M. Legault, John R. Green, Vincent G. Guida, and Joseph J. Vitaliano (node #15)

Background

The northern shrimp, *Pandalus borealis*, has a discontinuous distribution throughout the North Atlantic, North Pacific, and Arctic Oceans. In the Gulf of Maine, northern shrimp populations comprise a single stock (Clark and Anthony 1980), which is concentrated in the southwestern region of the Gulf (Haynes and Wigley 1969). *P. borealis* occurs as far south as New Jersey on the continental slope (William 1984). *Dichelopandalus leptocerus* can be found from Newfoundland to North Carolina, from estuaries to the continental slope (Williams 1984). While *D. leptocerus* is not exploited commercially, is an important forage item for a number of fisheries species including monkfish, spiny dogfish, various skate species, red hake, silver hake, and black sea bass (Bowman and Michaels 1984; Bowman *et al.* 2000; Steimle *et al.* 2000). It is the principal non-crangonid shrimp species in the region outside of the Gulf of Maine. *Pasiphaea multidentata*, a circumpolar bathypelagic species largely restricted to the Gulf of Maine in our area, may also play a substantial role as a forage species and consumer of zooplankton and micronekton along with *D. leptocerus* (Cartes 1993, Frank and Widder 1997). Additional caridean and penaeid shrimp species (e.g., *Lebbeus* spp., *Spirontocaris* spp., *Parapenaeus politus*) occur at depths approaching 200 m and beyond in all subregions and in shallower waters of the Gulf of Maine (Williams 1984), but are probably not in sufficient numbers to be important in terms of the system energy budget. The same is likely true of southern penaeids (white, pink, brown, and rock shrimp: *Litopenaeus setiferus*, *Farfantepenaeus duodorum*, *F. aztecus*, and *Sicyonia brevirostris*, respectively) that may occur in small numbers as far north as southern New England (Williams 1984). Unlike most other decapod shrimps, the very abundant and widespread crangonids (e.g., *Crangon septemspinosa*, *Pontophilus* spp.) are readily captured and assessed by grab sampling, and are therefore included with other such species in the macrobenthos - crustaceans node (Section 8 of this document) rather than here. The species we categorized as shrimp are given in Table 11.1.

Data Sources

Stock assessment for Gulf of Maine northern shrimp reviewed in SARC 36 (SARC 2003) used commercial landings data, Northern Shrimp Technical Committee summer shrimp survey data, and unpublished data from NEFSC Benthic Habitat cruises.

Quantitative Approach for Biomass Estimates

A Collie-Sissenwine analysis was used to estimate biomass of northern red shrimp (*P. borealis*) in the Gulf of Maine. This analysis is based on relating the annual changes in survey abundance for both recruiting shrimp and fully recruited shrimp to the annual catches in order to estimate biomass of northern shrimp in the Gulf of Maine for years 1985 to 2003. The assessment was confirmed using surplus production, a different modeling approach which produced qualitatively similar results. The Collie-Sissenwine model biomass estimates for years 1996-2000 were averaged and then multiplied by 1.5 to account for other species of shrimp. The

resulting total shrimp biomass (mt) was divided by the area of Gulf of Maine (km²) to produce a total shrimp biomass value in units of g m⁻² (Table 11.2).

Biomass Results

As shrimp are not harvested commercially outside of the Gulf of Maine in the NEUS Ecosystem, this type of analysis could not be used for biomass estimates of shrimp in other subregions (principally *D. leptocerus*). A mean density estimate for *D. leptocerus* was made (0.0171 g m⁻² or 0.0075 individuals m⁻², Guida unpublished) from 2 m beam trawl catches at 38 stations during summer and fall cruises to the outer shelf near Hudson Canyon, along the border between the Mid-Atlantic and Southern New England subregions. While this density is based upon a very limited dataset from a very small portion of the entire region, it is comparable in magnitude to the only published density for this species in the NEUS Ecosystem: 0.0035 individuals m⁻² (no biomass data provided) calculated from data on a year-round study performed in Penobscot Bay, Gulf of Maine (Stevenson and Pierce 1984). Semiquantitative data from epibenthic sled collections in nearshore waters off New York Harbor also indicate densities in the range of 10⁻³ to 10⁻² individuals m⁻² (Guida, unpublished). We have therefore chosen to adopt 0.0171 g m⁻² as an estimate of shrimp biomass for Georges Bank, Southern New England, and the Mid-Atlantic Bight subregions.

Production/Growth/Reproduction

Production was estimated using a P:B ratio of 1.5 based on the assumption that as large, active invertebrates, P:B should resemble that of squid and megabenthos - other. Production was estimated to be 0.1695 * 1.5 = 0.254214 g m⁻² yr⁻¹ in the case of the GOM.

Consumption

Consumption was estimated using a C:B ratio of 13.5 based again on the assumption that shrimp should resemble other large benthic invertebrates. Consumption was estimated to be 0.1695 * 13.5 = 2.2883 g m⁻² yr⁻¹ in the case of the GOM.

Respiration

We have chosen to estimate respiration values for the macrobenthic nodes from other composite parameters for the same groups:

$$(EQ. 11.1) \quad R = C \times E_A \times 0.65,$$

where R is respiration, C is consumption, E_A is assimilation efficiency, and 0.65 represents the fraction of assimilated energy that is typically respired by ectotherms (Parry 1983). Values for assimilation efficiencies for this purpose were derived from Valiela (1995). Thus, respiration was estimated to be 2.2883 * 0.7 * 0.65 = 1.0412 g m⁻² yr⁻¹ in the case of the GOM (Table 11.3).

Example Results

Values for biomass density, production, consumption, and respiration for shrimp and shirmp-like species in each of the four subregions are summarized in Table 11.3.

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Table 11.1. Species list of shrimp.

Common Name	Scientific Name
Northern red shrimp	<i>Pandalus borealis</i>
Other northern shrimps	<i>P. propinquus</i> , <i>P. montagui</i>
Bristlebeaked shrimp	<i>Dichelopandalus leptocerus</i>
Glass shrimp	<i>Pasiphaea multidentata</i>

Table 11.2. Estimates of biomass for shrimp species listed in Table 11.1 in the Gulf of Maine based on model results for northern red shrimp (*P. borealis*).

Fishing Year	Biomass (mt)	
1996	15,516	
1997	11,008	
1998	6,728	
1999	5,791	
2000	5,658	
	8,940	Average for Northern Red Shrimp (mt)
	1.5	Multiplier for Other Shrimp Species
	13,410	Total Shrimp Biomass (mt)
	79127.95	Gulf of Maine Area (km ²)
	0.1695	Biomass (g m ⁻²)

Table 11.3. Rate values for shrimp.

Subregion	Biomass Density (g m ⁻²)	Production (g m ⁻² yr ⁻¹)	Consumption (g m ⁻² yr ⁻¹)	Respiration (g m ⁻² yr ⁻¹)
GOM	0.1695	0.25425	2.2883	1.0412
GB	0.0171	0.02565	0.2309	0.1050
SNE	0.0171	0.02565	0.2309	0.1050
MAB	0.0171	0.02565	0.2309	0.1050

12. Larval and Juvenile Fish

John R. Green and Donna L. Johnson (node #16)

Background

Larval fish included in this study represent a wide variety of taxonomic groups and growth forms that change with season and location. Although fish larvae are present in all seasons, abundances decrease in fall and winter when the most numerous larvae are elongated clupeid types. During the spring and early summer gadiform and flatfish larvae are at their most numerous. Larval myctophids are numerous and sometimes dominant, although the adults are distributed in deeper water off the continental shelf.

Data Sources & Sampling Procedures

Larval fish biomass was derived from the Marine Resources Monitoring, Assessment and Prediction (MARMAP) sampling program conducted from 1977-87 on the U.S. continental shelf from Cape Hatteras, North Carolina to the Gulf of Maine (Sherman 1980, Morse 1982, Sherman 1986). Double-oblique 61 cm bongo ichthyoplankton and zooplankton sampling tows were taken from the surface to a maximum depth of 200 m or from within 5 meters of the bottom. The sampler was fitted with 0.505 mm mesh nets for ichthyoplankton and 0.333 mm nets for zooplankton. The flowmeter was used as a measure of filtration efficiency for each sample. Ichthyoplankton samples were sorted, identified, and enumerated according to the procedures outlined by Jossi and Marak (1983). Larval fish were identified to the lowest taxon possible and measured to the nearest 0.1 mm standard length (SL). For a summary of MARMAP operations see Sibunka and Silverman (1984, 1989).

Mean-Abundance Procedures

The number of larvae caught was transformed to the number of individuals under 10 m² of sea-surface area based on the maximum tow depth and volume filtered by the bongo net:

$$(EQ. 12.1) \quad N = 10 * C * M * B^{-1} * D^{-1}$$

where N represents the standardized abundance; C represents the number of larvae collected in the sample; M represents the maximum tow depth (meters); B represents the aperture of the bongo frame; and D represents the total distance the net was towed in meters from the calibrated flowmeter (Smith and Richardson 1977). The mean abundance and its variance were calculated by Pennington's (1983) method based on the Delta (Δ) distribution. For each station, catch values were standardized to the number of individuals under 10 m² surface area. The Delta distribution of catch frequencies (Aitchison 1955) was used to provide unbiased estimates of sample means from mean catch calculations and its variance using zero tows (Berrien, *et al.* 1981; Pennington 1983).

Larval Fish Biomass

Delta mean abundances (number/10 m²) of all larvae were extracted by 1 mm SL increments. Dry weight was estimated for each 1 mm abundance group averaged over all seasons of sampling using the length to weight relationship:

$$(EQ\ 12.2) \quad \text{LogDW} = -4.152\text{LogSL}^{1.186}$$

where DW is dry weight in ug and SL is standard length in mm. The coefficient of SL (1.186) and the intercept are the means of the those parameters from length weight relationships in Laurence (1979) based on laboratory-reared larvae of seven species of fish including a variety of growth forms. Larval weights are rarely given in the literature as wet weight, thus dry weight was assumed to be equal to 10% of wet weight, as were other planktonic forms.

Production and Consumption

For purposes of this study, consumption rates used for larvae are based on the average growth rate observed for larval gadids taken from laboratory studies at the NMFS Narragansett laboratory (Laurence, 1978) and unpublished field observations. Growth (i.e., production) was estimated at 0.04 day⁻¹ based on an assumption of growth consistent with that of juvenile cod (Peck *et al.* 2003). These values were then scaled to provide an annual estimate. This produced a P:B ratio of 15, similar to micronekton.

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13. Small Pelagics (commercial, other, squid, anadromous) and Mesopelagics

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Background and Estimation Approach

Five categories of small pelagic fish were assessed using a survey swept area biomass expansion approach. Categories included small pelagics – commercial; small pelagics – other; squid, anadromous, and mesopelagic fishes (Table 13.1). Time series of spring and autumn research bottom trawl survey swept area biomass were produced for the 1996-2000 period. Informative gamma priors for weighting coefficients were developed from sources in the literature for the various categories by using available values (Table 13.2; Edwards 1968; Harley *et al.* 2001). Specific priors were developed for herring, mackerel, butterfish, sand lance, and anadromous, while general priors were developed for the squid, mesopelagic, and pelagic - other categories (Table 13.2). In addition, species-specific weighting coefficients were developed from stock assessments for herring, mackerel, and butterfish to be used as maximum likelihood estimates for these species. Linear regressions of spring and autumn survey swept area biomass on stock biomass were used to estimate the coefficient for each of the three stocks.

Priors used in the analysis were based on a gamma distribution where:

$$(EQ. 13.1) \quad F(x) = \frac{u^r x^{r-1} e^{-ux}}{\Gamma(r)}; \quad x > 0$$

where u is the mean and r is a shape parameter.

Priors for herring and mackerel were developed from weighting coefficients provided in Edwards (1968) for herring and argentine. The value for butterfish was taken as the average for butterfish and redfish from the same source. The prior for sand lance was available from Harley *et al.* (2001) and for the anadromous category from Edwards (1968) for alewife. A general prior was developed for the rest of the categories, taken as the average for herring, argentine, butterfish, and alewife (Edwards 1968). A Bayesian model framework was developed for each pelagic category, a CV of 25% was assumed for the r and u parameters of the gamma distributions for each category, and informative priors were calculated (Figure 13.1 and Table 13.3). In the case of herring, mackerel, and butterfish, recent estimates of weighting coefficients from the linear regression analysis were additionally provided as specific maximum likelihoods used to modify priors. Biomass estimates for all other categories were calculated based only on priors.

A WinBUGS (Spiegelhalter *et al.* 2003) model was produced for each pelagic category or for each single stock of pelagic fish, and average values (1996-2000) of swept area biomass for spring and autumn for each ecoregion were input. Two MCMC chains (Monte Carlo Markov Chains) were initiated for each run with a 10,000 iteration burn in period and a 100,000 iteration output period. Total biomass for each ecoregion was produced (Table 13.4), along with summary statistics including mean, sd, median, quartiles, and 80% and 95% CI's. In addition, trajectories for each variable and posterior distributions were output as cross checks on model performance. Results for herring, mackerel, and butterfish were summed to produce total biomass estimates for the pelagic - commercial category, and sand lance and the pelagic - other category were summed to produce the total for the pelagic - other category.

Production

Production for herring and mackerel was estimated from age-based data. Instantaneous growth rates were estimated from mean weight at age data, multiplied by average biomass, and summed across ages to obtain estimates of total production for 1996-2000. These values were annualized and converted to g m^{-2} (Table 13.4). The values were divided by annual biomass to obtain P:B ratios for mackerel and herring. Butterfish production was estimated from surplus production methods. Production to biomass ratios were used to calculate production for the other small pelagic categories. The butterfish P:B ratio (0.95) was used to calculate production for the pelagic - other, mesopelagic, and squid groups. The herring P:B ratio (0.42) was used for the anadromous group (Table 13.4).

Consumption

Consumption to biomass ratios for small pelagic and demersal fish were investigated by exploring the approach used in Sissenwine *et al.* (1984). In this study C:B ratios for six Georges Bank species were calculated based on theoretical considerations, ranging between 3.2 and 4.9 (Sissenwine *et al.* 1984). New calculations for GOM fishes suggest that these estimates may be too high; Palomares and Pauly's (1998) estimates ranged between 1.2 and 3.9 (Table 13.5). Ratios for pelagic and demersal fish used to balance the GOM Ecopath and EcoNetwrk models were based on estimates from the NEFSC food habits database. These estimates utilized the Eggers (1977) equation for consumption, and all the ratios were less than those in the Sissenwine *et al.* (1984) and Palomares and Pauly (1998) approaches.

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Table 13.1. List of species in the pelagic category.

Pelagics				
Pelagic-Commercial	Squid	Anadromous	Pelagic-Other	
<i>Clupea harengus</i>	<i>Cephalopoda</i>	<i>Alosa pseudoharengus</i>	<i>Etrumeus teres</i>	<i>Scomberesox saurus</i>
<i>Scomber scombrus</i>	<i>Illex illecebrosus</i>	<i>Alosa aestivalis</i>	<i>Brevoortia tyrannus</i>	<i>Decapterus macarellus</i>
<i>Peprilus triacanthus</i>	<i>Loligo pealeii</i>	<i>Alosa sapidissima</i>	<i>Osmerus mordax</i>	<i>Selar crumenophthalmus</i>
		<i>Alosa mediocris</i>	<i>Argentina silus</i>	<i>Decapterus punctatus</i>
Meso-Pelagic			<i>Menidia menidia</i>	<i>Trachurus lathami</i>
<i>Myctophidae</i>			<i>Ammodytes dubius</i>	<i>Ariomma bondi</i>
<i>Maurolicus sp.</i>			<i>Anchoa mitchilli</i>	<i>Opisthonema oglinum</i>
			<i>Anchoa hepsetus</i>	<i>Sardinella aurita</i>
			<i>Ablennes hians</i>	<i>Hemiramphus brasiliensis</i>
			<i>Scomber japonicus</i>	<i>Mugil cephalus</i>
			<i>Selene setapinnis</i>	<i>Mugil curema</i>

Table 13.2. Values for weighting coefficients from Edwards (1968) and Harley *et al.* (2001) and average values used for developing priors for each category.

Category	Species	Coefficient	Average
Pelagic - commercial			
Herring and mackerel	Argentine	0.018	0.014
	Herring	0.01	
Butterfish	Butterfish	0.07	0.17
	Redfish	0.27	
Pelagic - other			
	Herring	0.01	0.08
	Argentine	0.018	
	Butterfish	0.07	
	Alewife	0.22	
	Sand lance	0.00087	0.00087
Squid			
	Herring	0.01	0.08
	Argentine	0.018	
	Butterfish	0.07	
	Alewife	0.22	
Anadromous			
	Alewife	0.22	0.22
Meso-pelagic			
	Herring	0.01	0.08
	Argentine	0.018	
	Butterfish	0.07	
	Alewife	0.22	

Table 13.3. Priors for gamma distributions for small pelagic fishes and squids

Pelagic - commercial	Herring	$r \sim \text{gamma}(16,4)$	$u \sim \text{gamma}(16,0.056)$
	Mackerel	$r \sim \text{gamma}(16,4)$	$u \sim \text{gamma}(16,0.056)$
	Butterfish	$r \sim \text{gamma}(16,4)$	$u \sim \text{gamma}(16,0.680)$
Pelagic - other	Sand lance	$r \sim \text{gamma}(16,4)$	$u \sim \text{gamma}(16,0.0035)$
	Other	$r \sim \text{gamma}(16,4)$	$u \sim \text{gamma}(16,0.320)$
Squid	Squid	$r \sim \text{gamma}(16,4)$	$u \sim \text{gamma}(16,0.320)$
Anadromous	Anadromous	$r \sim \text{gamma}(16,4)$	$u \sim \text{gamma}(16,0.880)$
Mesopelagic	Mesopelagic	$r \sim \text{gamma}(16,4)$	$u \sim \text{gamma}(16,0.320)$

Table 13.4. Estimates of average biomass and production by group and region during 1996-2000.

Biomass ($\text{g m}^{-2} \text{yr}^{-1}$)						
	Pel - comm	Pel - other	Squid	Meso	Anadromous	Total
MAB	5.998476	3.92701	1.424743	0.002302	0.112047	11.46457731
SNE	13.88781	1.151342	2.728052	0.001314	0.160336	17.92885055
GB	9.946622	1.054368	0.962301	3.66E-05	0.037755	12.00108276
GOM	4.545072	1.060215	0.134569	6.82E-05	0.077245	5.81716827
Total	8.280098	1.777949	1.267477	0.000928	0.100272	11.42672373

Production ($\text{g m}^{-2} \text{yr}^{-1}$)						
	Pel - comm	Pel - other	Squid	Meso	Anadromous	Total
MAB	2.217167	3.732137	1.354042	0.002188	0.047618	7.353151661
SNE	5.04278	1.094208	2.592676	0.001249	0.06814	8.799052399
GB	3.434282	1.002046	0.914548	3.48E-05	0.016045	5.366956876
GOM	1.892098	1.007603	0.127892	6.49E-05	0.032827	3.060484459

Table 13.5. Ratios for C:B for GOM-GB species from the Palomares and Pauly (1997) equation.

	W~	T'	A	log(C/B)	C/B
Atlantic mackerel	1000	3.55682	2.65	0.582798	3.82647
Herring	300	3.55682	1.5	0.594016	3.92659
Bluefish	11363	3.55682	2.12	0.323488	2.106142
BFT	545454	3.55682	7	0.38555	2.429683
Cod	90901	3.55682	1.5	0.0878	1.224053
Haddock	11363	3.55682	1.4	0.263728	1.835387
Spiny dogfish	5000	3.55682	1.6	0.353058	2.254542

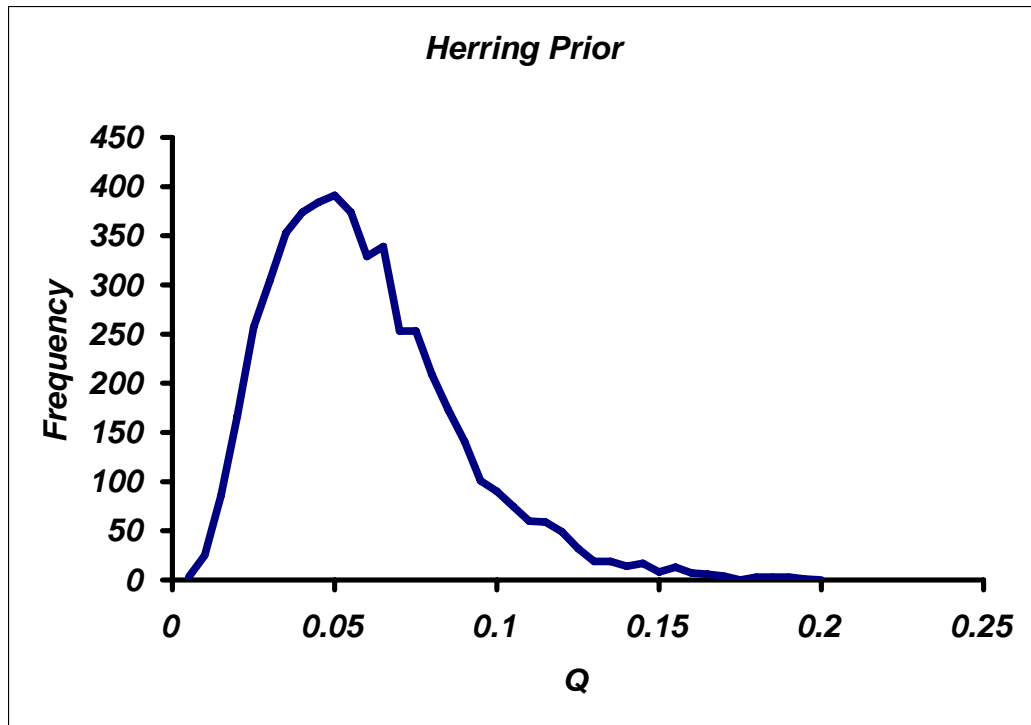


Figure 13.1. Example prior for Q on herring developed from values for herring and argentine from Edwards (1968) and stock abundance data.

14. Demersals (benthivores, omnivores, piscivores) and Medium Pelagics

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Background

Three groups of demersal species were formed based on feeding preferences described in Collette and Klein-MacPhee (2002). These are: benthivores, piscivores, and omnivores (includes all others). The demersal benthivore group was composed of species that primarily feed on benthic prey. This group included gadiformes, elasmobranchs, pleuronectiformes, perciformes, scorpaeniformes, and other benthivores (Table 14.1). The demersal piscivore group included species that feed primarily on fishes. This group included gadiformes, elasmobranchs, and other piscivores (Table 14.2). The unclassified demersals was a large group composed of either omnivorous species that fed opportunistically on both benthos and fish (Table 14.3), or unclassified southern demersal species whose food habits were not reported in Collette and Klein-MacPhee (2002; Table 14.4).

Data Sources

Annual research survey data were collected from 1968-2003 to estimate demersal and pelagic biomasses using a stratified random sampling design (Azarovitz 1981).

Quantitative Approach for Biomass Estimates

Survey Catchability

Research survey catchability varies among species and groups of species. If it were known for a given species or group, survey catchability (Q) would provide a direct estimate of absolute biomass (B) based on the survey index value (I):

$$(EQ. 14.1) \quad B = \frac{I}{Q}$$

We assumed that the average survey catchability for each demersal or pelagic species group was constant and estimable. Seasonal estimates of average survey catchability were made for each species group during spring and autumn using the Bayesian estimation approach described below. The seasonal estimates of Q were then applied to spring and autumn survey swept-area biomass indices during 1968-2003 to produce an estimate of absolute biomass for each species group and season using Equation 14.1. The seasonal estimates of absolute biomass were then averaged to produce an estimate of average annual biomass for each species group during 1968-2003.

Bayesian Estimation Approach

A priori, it was recognized that there were few direct observations to estimate the average catchability of many species groups. Given this lack of information, we chose to use a Bayesian estimation approach to incorporate information on catchability from previous studies. This

enabled us to use both prior information and observed data to estimate seasonal catchabilities for species groups. A probability model (likelihood) was developed for observed catchability data where both model parameters and observed data were assumed to be random variables. The joint probability distribution for model-based catchability estimate (Q) and catchability data (D), denoted by $p(Q, D)$, depended on the prior distribution of model parameters (see Informative Priors below), denoted by $p(Q)$, and the likelihood of observing the data (see Likelihood of Catchability Observations below), denoted by $p(D | Q) \equiv L(D | Q)$.

$$(EQ. 14.2) \quad p(Q | D) = p(Q)p(D | Q)$$

Applying Bayes' rule for the conditional probability of model parameters given the data, the posterior distribution of model parameters was $p(Q | D)$

$$(EQ. 14.3) \quad p(Q|D) = \frac{p(Q,D)}{p(D)} = \frac{p(Q)p(D|Q)}{p(D)}$$

where the integrated likelihood $p(D)$ was the constant

$$(EQ. 14.4) \quad p(D) = \int p(Q)p(D|Q)dQ$$

Since $p(D)$ was constant with respect to the model parameters (which have been integrated out of the expression), the posterior distribution of model parameters is proportional to the product of the (informative) prior and the likelihood

$$(EQ. 14.5) \quad p(Q|D) \propto p(Q)p(D|Q)$$

Markov Chain Monte Carlo (MCMC) simulation (Gilks *et al.* 1996) was applied to numerically generate posterior samples from Equation. 14.5. MCMC simulates a random walk through the set of possible catchability values that converges to a stationary distribution that is exactly the posterior distribution of Q. This simulation was equivalent to numerically integrating Equation 14.3. We used the WINBUGS 1.4 software for performing the MCMC calculations (Spiegelhalter *et al.* 2003). For each species group, two simulated chains of length 110,000 posterior samples of Q were generated. In the first chain the coefficient of variation (CV) for Q was 50% while $CV[Q] = 75\%$ in the second chain. The first 10,000 samples of both chains were discarded to burn them in (i.e., to eliminate dependence on the initial value of Q). Of the remaining 100,000 samples in each chain, every other sample was discarded to eliminate the possibility of autocorrelation. This left 100,000 posterior samples of Q for inference (50,000 from each chain). Inferences about the estimated absolute biomasses of species groups were based on this numerical integration of $p(Q | D)$. For example, the expected value of biomass of the jth species group (B_j) in a given year was calculated from $N=100,000$ posterior samples of the survey catchability of the jth species group (Q^1, Q^2, Q^3, \dots) as

$$(EQ. 14.6) \quad E[B_j | D] \approx \frac{1}{N} \sum_{T=1}^N B_j(Q^T)$$

Informative Priors

Prior information on NEFSC research survey catchabilities was available from two sources: Edwards (1968) and Clark and Brown (1977). In the former study, Edwards developed estimates of NEFSC survey catchability for 27 species based on their seasonal availability within the survey region and their vulnerability to the survey trawl gear. These survey catchability estimates were scaled to adjust survey swept-area biomass indices to absolute biomasses. In Clark and Brown's study, estimates of NEFSC autumn survey catchability were developed for several species using estimates of fishing mortality, total catch and stock size, and relative survey abundance indices. These catchability estimates were appropriate for scaling survey mean catch biomass per tow and were rescaled to swept-area values for comparison with Edwards' results.

The informative prior for catchabilities of demersal species groups was assumed to be a gamma distribution with shape (r) and scale (μ) parameters.

$$(EQ. 14.7) \quad p(Q|r, \mu) \sim \text{Gamma}(r, \mu) = \mu^r Q^{r-1} \frac{e^{-\mu Q}}{\Gamma(r)} \quad \text{for } Q > 0$$

This choice provided a flexible positive distribution with mean equal to $E[Q] = r/\mu$ and coefficient of variation equal to $CV[Q] = r^{-0.5}$.

For the demersal species groups, the expected value of the informative catchability prior was determined from Edwards' (1968) catchability estimate for the "all others" species group ($Q = 0.16$) and Clark and Brown's (1977) untransformed catchability estimate for "other finfish" ($Q = 0.13$, $CV = 31\%$). These two values were chosen because they represented general groups of species that were not actively targeted by commercial fisheries at that time. We set the expected value of the catchability prior to equal the average of the two catchability estimates so that $E[Q] = 0.145$. Given the expected value of Q , the $CV[Q]$ was assumed to be 50%. This implied that the informative prior was more variable than Clark and Brown's estimate of survey Q .

The shape and scale parameters of the informative prior for demersal species groups were also parameters in the estimation model. Both were assumed to be distributed as a gamma random variable with parameters chosen to match the values of $E[Q]$ and $CV[Q]$. In particular, the hyperprior for the shape parameter r was distributed as $\text{Gamma}(16, 4)$. This implied that the expected value of r was $E[r] = 4$, with $CV[r] = 25\%$. The hyperprior for the scale parameter μ was distributed as $\text{Gamma}(16, 0.58)$. This implied that the expected value of μ was $E[\mu] = 27.6$ with $CV[\mu] = 25\%$. These choices led to $E[r]/E[\mu] = E[Q] = 0.145$ and $CV[Q] = 50\%$.

Observed Catchability Data

There were two sources of survey catchability observations (Q^{OBS}) for the demersal species groups: Edwards (1968); and catchability observations derived from stock assessment data. Edwards (1968) provided survey catchability data for a total of 23 species (Table 14.2). Of these, the same catchability data was used for benthivore and omnivore elasmobranchs given the

similarity in their benthic habitats and body shapes. These catchabilities were used as average values for autumn and spring since Edwards included seasonal availability as a calculation factor. There were a total of 12 catchability observations derived from assessment data (Table 14.2). All of these were derived from age-structured assessment information (NEFSC 2002, NEFSC 2003a, NEFSC 2003b, Terceiro 2003), with the exception of spiny dogfish (*Squalus acanthias*, NEFSC 2003b). Separate catchability values for autumn and spring were derived by regressing survey swept-area biomass (thousand mt) on stock biomass (thousand mt) over the assessment time period. The slopes of these regressions were the observed survey catchabilities. This approach was used for 11 stocks. Seasonal differences in catchability were apparent for some stocks (e.g., American plaice, *Hippoglossoides platessoides*), but not for others. For spiny dogfish, the assessment-based catchability was derived as the ratio of total spring survey swept-area biomass during 1990-2002 to total biomass estimated using the minimum trawl herding assumption (NEFSC 2003b, Tables B6.2 and B7.3) during the same period.

Likelihood of Catchability Observations

The likelihood of a single catchability observation was a gamma distribution (Equation 14.3) with shape and scale parameters set by the informative priors. Seven demersal subgroups did not have any catchability observations (Table 14.2). These were: other benthivores, other omnivores, and the five unclassified southern demersal species subgroups. For the pelagic groups, only the pelagic commercial finfish group had catchability observations (Table 14.2). Catchabilities of the remaining groups that had no catchability observations were determined by their informative priors. The joint likelihood of a total of n catchability observations (Q_i) was

$$(EQ. 14.8) \quad L(D|\theta) = \left(\frac{\mu^r}{\Gamma(r)} \right)^n \prod_{i=1}^n Q_i^{r-1} e^{-\mu Q_i}$$

Average Biomass Production

Average biomass production per unit area was computed for each species group, region, and year. There were some obvious outliers due to variability in survey catches. These outliers had a disproportionate influence on average biomass. To identify outliers in an objective manner we computed biomass production anomalies (B^{ANOM}) for each group and region using the median ($B_{0.5}$) and standard deviation (σ_B) of the observed values (B^{OBS})

$$(EQ. 14.9) \quad B^{ANOM} = \frac{B_{0.5} - B^{OBS}}{\sigma_B}$$

We removed outliers based on the biomass production anomalies. For demersal species groups, an observed value was an outlier if $B^{ANOM} > 3$. Applying this criterion led to removal of 10 outliers out of a total of 864 observed values ($\approx 1\%$).

Average biomass production per unit area (grams per square meter) was computed for each species group and region over the period 1968-2003. This was done to see if there were regional differences in biomass production by individual species groups. Average total biomass production for demersal species groups was also computed along with the percent contribution of

each group to the total. This was expected to show whether the production of demersal biomass differed among regions. Last, the average total production of demersal biomass was computed for each region to determine differences in total biomass production among regions.

Example Results

Average biomass production

Total demersal biomass production differed among regions (Figure 14.1). On average, Georges Bank had the highest demersal biomass (14 g m^{-2}) while the Gulf of Maine had the lowest (10 g m^{-2}). The Mid-Atlantic Bight had the most variability in demersal biomass and the Gulf of Maine had the least variability. Overall, total demersal biomass was less variable than biomass for the individual demersal groups.

Biomass production by the individual demersal groups also differed among regions (Figure 14.1). The highest average benthivore biomass was in the Mid-Atlantic Bight (5 g m^{-2}) while the lowest was in Southern New England (2 g m^{-2}). Average piscivore biomass ranged from a low of 6 g m^{-2} in the Mid-Atlantic Bight and Georges Bank to a high of 8 g m^{-2} in Southern New England. The highest average omnivore biomass was on Georges Bank (5 g m^{-2}). In comparison, omnivore biomass was only 1 g m^{-2} in the Gulf of Maine and the Mid-Atlantic. Benthivore biomass varied substantially in each region with CVs ranging from 35-50%. Piscivore and omnivore biomasses were also highly variable, with CVs of 40-65%. The exception was the Gulf of Maine piscivore biomass which was the least variable of all the groups (CV=23%).

Individual demersal groups contributed differing percentages to the total demersal biomass by region (Figure 14.1). The piscivore group was the dominant group in each region. Its contribution to total demersal biomass ranged from a low of 37% for Georges Bank to a high of over 60% in the Gulf of Maine and Southern New England. The benthivore group was the 2nd dominant group in the Gulf of Maine (31%) and Mid-Atlantic Bight (41%). These regions also had the lowest percent composition of omnivores (9%). In comparison, the omnivore group was 2nd dominant on Georges Bank (34%) and in Southern New England (20%).

Production/Growth/Reproduction

Production for demersals and medium pelagics was estimated using age-based data for a small number of assessed stocks to confirm literature values for the P:B ratio (Cohen *et al.* 1982; Sissenwine 1987; Savenkoff *et al.* 2004). Two approaches were used to estimate the P:B ratios from virtual population analysis results: age-based growth and a production model. The age-based growth approach computed the change in weight at age for each cohort in a given year and multiplied these values by the average biomass for that age. Summing these values produced an estimate of production which was then divided by the beginning of the year biomass to generate an estimate of the P:B ratio. The production model approach calculated production as the total catch plus the change in biomass each year and then divided that by the biomass to produce a P:B ratio. Results for Georges Bank cod, haddock and yellowtail flounder ranged from 0.34 to 0.48 for the age-based growth approach and ranged from 0.35 to 0.59 for the production model approach. These results agreed in general with the literature values for demersals and medium

pelagics. The selected values for the P:B ratio varied by group: demersal benthivores and omnivores had a ratio of 0.45 while demersal piscivores and medium pelagics had a ratio of 0.55.

Consumption

Consumption was estimated using the methods described in Section 22: Consumption and Diet Composition Matrix, based on NEFSC research survey observations. Resulting C:B ratios for the Gulf of Maine ecoregion were on the order of 0.6 to 3.0.

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Table 14.1. List of species in the demersal benthivore category.

Demersal Benthivores				
Gadiformes	Elasmobranchs	Perciformes	Scorpaeniformes	Others
<i>Melanogrammus aeglefinus</i>	<i>Dasyatis centroura</i>	<i>Macrorhamphosus scolopax</i>	<i>Pontinus longispinis</i>	<i>Myxine glutinosa</i>
<i>Urophycis chuss</i>	<i>Etmopterus princeps</i>	<i>Synagrops bellus</i>	<i>Sebastes fasciatus</i>	<i>Antigonia capros</i>
<i>Urophycis regia</i>	<i>Dasyatis say</i>	<i>Micropogonias undulatus</i>	<i>Helicolenus dactylopterus</i>	<i>Opsanus tau</i>
<i>Antimora rostrata</i>	<i>Myliobatis freminvillei</i>	<i>Synagrops spinosus</i>	<i>Helicolenus maderensis</i>	<i>Dibranchius atlanticus</i>
<i>Enchelyopus cimbrius</i>	<i>Torpedo nobiliana</i>	<i>Orthopristis chrysoptera</i>	<i>Artediellus sp.</i>	<i>Ogcocephalus corniger</i>
<i>Brosme brosme</i>	<i>Raja eglanteria</i>	<i>Stenotomus chrysops</i>	Cottidae	<i>Chlorophthalmus sp</i>
<i>Gaidropsarus ensis</i>	<i>Leucoraja garmani</i>	<i>Epigonus pandionis</i>	<i>Triglops murrayi</i>	<i>Chlorophthalmus agassizi</i>
Macrouridae	<i>Malacoraja senta</i>	<i>Menticirrhus saxatilis</i>	<i>Myoxocephalus scorpius</i>	<i>Gonostoma bathyphilum</i>
<i>Nezumia bairdi</i>	<i>Dasyatis americana</i>	<i>Pogonias cromis</i>	<i>Myoxocephalus octodecemspinosus</i>	<i>Gonostoma atlanticum</i>
<i>Macrourus berglax</i>	<i>Rhinoptera bonasus</i>	<i>Bairdiella chrysoura</i>	<i>Hemirhamphus americanus</i>	<i>Gonostoma elongatum</i>
<i>Coelorhynchus carminatus</i>		<i>Leiostomus xanthurus</i>	<i>Aspidophoroides monopterygius</i>	<i>Vinciguerria sp</i>
<i>Otophidium omostigmum</i>		<i>Howella sherborni</i>	<i>Myoxocephalus aeneus</i>	<i>Polymetme thaeocoryla</i>
<i>Ophidion marginatum</i>	Pleuronectiformes	<i>Lopholatilus chamaeleonticeps</i>	<i>Liparis inquilinus</i>	<i>Chauliodus danae</i>
<i>Lepophidium profundorum</i>	<i>Poecilopsetta beani</i>	<i>Tautoglabrus adspersus</i>	<i>Eumicrotremus spinosus</i>	<i>Parasudis truculenta</i>
<i>Malacocephalus occidentalis</i>	<i>Hippoglossoides platessoides</i>	<i>Tautoga onitis</i>	<i>Prionotus carolinus</i>	<i>Xenodermichthys copei</i>
<i>Ophidion grayi</i>	<i>Paralichthys oblongus</i>	<i>Astroscoptes guttatus</i>	<i>Prionotus evolans</i>	<i>Polymixia lowei</i>
<i>Ophidion welshi</i>	<i>Limanda ferruginea</i>	<i>Lumpenus lumpretaeformis</i>	<i>Peristedion miniatum</i>	<i>Polymixia nobilis</i>
	<i>Pseudopleuronectes americanus</i>	<i>Lumpenus maculatus</i>	Triglidae	<i>Hoplostethus occidentalis</i>
	<i>Glyptocephalus cynoglossus</i>	<i>Ulvaria subbifurcata</i>	<i>Careproctus ranula</i>	<i>Gephyroberyx darwini</i>
	<i>Scophthalmus aquosus</i>	<i>Mullus auratus</i>	<i>Prionotus paralatus</i>	<i>Saurida brasiliensis</i>
	<i>Citharichthys arcifrons</i>	<i>Lycodes reticulatus</i>		<i>Bagre marinus</i>
	<i>Monolene sessilicauda</i>	<i>Lycenchelys verrilli</i>		<i>Opsanus pardus</i>
	<i>Etropus microstomus</i>	<i>Cryptacanthodes maculatus</i>		<i>Porichthys plectrodon</i>
	<i>Trinectes maculatus</i>	<i>Anarhichas lupus</i>		
		<i>Macrozoarces americanus</i>		
		<i>Nesiarchus nasutus</i>		

Table 14.2. List of species in the demersal piscivore category.

Demersal Piscivores		
Gadiformes	Elasmobranchs	Others
<i>Merluccius albidus</i>	<i>Carcharhinus obscurus</i>	<i>Reinhardtius hippoglossoides</i>
<i>Merluccius bilinearis</i>	<i>Centroscyllium fabricii</i>	<i>Hippoglossus hippoglossus</i>
<i>Gadus morhua</i>	<i>Carcharhinus plumbeus</i>	<i>Paralichthys dentatus</i>
<i>Pollachius virens</i>	<i>Carcharias taurus</i>	<i>Trichiurus lepturus</i>
<i>Urophycis tenuis</i>	<i>Mustelus canis</i>	<i>Lophius americanus</i>
<i>Urophycis chesteri</i>	<i>Scyliorhinus retifer</i>	
Gadidae	<i>Squalus acanthias</i>	
<i>Merluccius sp.</i>	<i>Squatina dumeril</i>	

Table 14.3. List of species in the demersal omnivore category.

Demersal Omnivores	
Elasmobranchs	Others
<i>Dipturus laevis</i>	<i>Centropristis striata</i>
<i>Leucoraja ocellata</i>	
<i>Leucoraja erinacea</i>	
<i>Amblyraja radiata</i>	

Table 14.4. List of species in the unclassified southern demersal category.

Unclassified Southern Demersal Species			
Perciformes	Perciformes (Cont.)	Perciformes (Cont.)	Tetraodontiformes
<i>Schultzea beta</i>	<i>Epinephelus mystacinus</i>	<i>Halichoeres caudalis</i>	<i>Balistidae</i>
<i>Mycteroperca interstitialis</i>	<i>Apogon aurolineatus</i>	<i>Halichoeres poeyi</i>	<i>Parahollardia lineata</i>
<i>Centropristis ocyurus</i>	<i>Rypticus subbifrenatus</i>	<i>Halichoeres radiatus</i>	<i>Aluterus heudeloti</i>
<i>Centropristis philadelphica</i>	<i>Eucinostomus gula</i>	<i>Hemipteronotus novacula</i>	<i>Aluterus monoceros</i>
<i>Epinephelus inermis</i>	<i>Gerreidae</i>	<i>Lachnolaimus maximus</i>	<i>Aluterus schoepfi</i>
<i>Diplectrum bivittatum</i>	<i>Archosargus probatocephalus</i>	<i>Labridae</i>	<i>Aluterus scriptus</i>
<i>Diplectrum formosum</i>	<i>Perciformes</i>	<i>Chaetodontidae</i>	<i>Balistes vetula</i>
<i>Epinephelus adscensionis</i>	<i>Calamus bajonado</i>	<i>Chaetodon aculeatus</i>	<i>Canthidermis sufflamen</i>
<i>Epinephelus drummondhayi</i>	<i>Calamus calamus</i>	<i>Cryptotomus roseus</i>	<i>Monacanthus ciliatus</i>
<i>Epinephelus flavolimbatus</i>	<i>Calamus leucosteus</i>	<i>Nicholsina usta</i>	<i>Lactophrys bicaudalis</i>
<i>Epinephelus guttatus</i>	<i>Calamus nodosus</i>	<i>Scarus coeruleus</i>	<i>Lactophrys polygona</i>
<i>Epinephelus penna</i>	<i>Calamus penna</i>	<i>Sparisoma radians</i>	<i>Lactophrys quadricornis</i>
<i>Epinephelus nigritus</i>	<i>Calamus proridens</i>	<i>Scaridae</i>	<i>Lactophrys trigonus</i>
<i>Epinephelus niveatus</i>	<i>Diplodus argenteus</i>	<i>Mugil liza</i>	<i>Lactophrys triqueter</i>
<i>Epinephelus striatus</i>	<i>Diplodus holbrooki</i>	<i>Mugil gyrans</i>	<i>Canthigaster rostrata</i>
<i>Hemanthias vivanus</i>	<i>Lagodon rhomboides</i>	<i>Sphyræna barracuda</i>	<i>Sphoeroides dorsalis</i>
<i>Mycteroperca bonaci</i>	<i>Pagrus sedecim</i>	<i>Sphyræna borealis</i>	<i>Sphoeroides nephelus</i>
<i>Mycteroperca microlepis</i>	<i>Stenotomus caprinus</i>	<i>Sphyræna guachancho</i>	<i>Sphoeroides spengleri</i>
<i>Mycteroperca phenax</i>	<i>Sparidae</i>	<i>Opistognathus lonchurus</i>	<i>Sphoeroides testudineus</i>
<i>Mycteroperca venenosa</i>	<i>Cynoscion arenarius</i>	<i>Opistognathus maxillosus</i>	<i>Chilomycterus antillarum</i>
<i>Holanthias martinicensis</i>	<i>Cynoscion nebulosus</i>	<i>Bembrops gobioides</i>	<i>Chilomycterus atinga</i>
<i>Paranthias furcifer</i>	<i>Cynoscion nothus</i>	<i>Astroscopus y-graecum</i>	<i>Diodon holocanthus</i>
<i>Hemanthias aureorubens</i>	<i>Equetus acuminatus</i>	<i>Xenoccephalus egregius</i>	<i>Diodon hystrix</i>
<i>Serraniculus pumilio</i>	<i>Equetus lanceolatus</i>	<i>Kathetostoma albigutta</i>	<i>Tetraodontidae</i>
<i>Serranus annularis</i>	<i>Equetus punctatus</i>	<i>Clinidae</i>	<i>Sphoeroides pachygaster</i>
<i>Serranus atrobranchus</i>	<i>Equetus umbrosus</i>	<i>Hypsoblennius ionthas</i>	
<i>Serranus baldwini</i>	<i>Larimus fasciatus</i>	<i>Blenniidae</i>	
<i>Serranus notospilus</i>	<i>Menticirrhus americanus</i>	<i>Ammodytes americanus</i>	
<i>Serranus phoebe</i>	<i>Menticirrhus littoralis</i>	<i>Foetorepus agassizi</i>	
<i>Serranus subligarius</i>	<i>Sciaenops ocellatus</i>	<i>Dormitator maculatus</i>	
<i>Serranidae</i>	<i>Stellifer lanceolatus</i>	<i>Bathygobius soporator</i>	
<i>Rypticus bistrispinus</i>	<i>Sciaenidae</i>	<i>Gobiosoma bosc</i>	
<i>Priacanthus cruentatus</i>	<i>Eucinostomus argenteus</i>	<i>Gobiidae</i>	
<i>Pristigenys alta</i>	<i>Pseudupeneus maculatus</i>	<i>Uranoscopidae</i>	
<i>Apogon maculatus</i>	<i>Upeneus parvus</i>	<i>Anisotremus virginicus</i>	
<i>Apogon pseudomaculatus</i>	<i>Kyphosus sectatrix</i>	<i>Haemulon aurolineatum</i>	
<i>Caulolatilus cyanops</i>	<i>Chaetodipterus faber</i>	<i>Haemulon carbonarium</i>	
<i>Lutjanus analis</i>	<i>Chaetodon aya</i>	<i>Haemulon plumieri</i>	
<i>Lutjanus apodus</i>	<i>Chaetodon capistratus</i>	<i>Haemulidae</i>	
<i>Lutjanus buccanella</i>	<i>Chaetodon ocellatus</i>	<i>Acanthurus bahianus</i>	
<i>Lutjanus campechanus</i>	<i>Chaetodon sedentarius</i>	<i>Acanthurus chirurgus</i>	
<i>Lutjanus griseus</i>	<i>Chaetodon striatus</i>	<i>Acanthurus coeruleus</i>	
<i>Lutjanus jocu</i>	<i>Holacanthus bermudensis</i>	<i>Ariomma regulus</i>	
<i>Lutjanus synagris</i>	<i>Holacanthus ciliaris</i>	<i>Peprilus alepidotus</i>	
<i>Lutjanus vivanus</i>	<i>Holacanthus tricolor</i>	<i>Stromateidae</i>	
<i>Ocyurus chrysurus</i>	<i>Pomacanthus arcuatus</i>	<i>Trichiuridae</i>	
<i>Pristipomoides aquilonaris</i>	<i>Abudefduf saxatilis</i>	<i>Ruvettus pretiosus</i>	
<i>Rhomboplites aurorubens</i>	<i>Chromis enchrysurus</i>	<i>Lepidocybium flavobrunneum</i>	
<i>Lutjanidae</i>	<i>Chromis insolata</i>	<i>Pomacentrus variabilis</i>	
<i>Lobotes surinamensis</i>	<i>Pomacentrus leucostictus</i>	<i>Scombridae</i>	
<i>Cookeolus japonicus</i>	<i>Bodianus pulchellus</i>	<i>Gempylus serpens</i>	
<i>Caulolatilus microps</i>	<i>Clepticus parrae</i>	<i>Cubiceps pauciradiatus</i>	
<i>Caulolatilus chrysops</i>	<i>Decodon puellaris</i>	<i>Seriola fasciata</i>	
<i>Caulolatilus intermedius</i>	<i>Halichoeres bathyphilus</i>	<i>Haemulon striatum</i>	
<i>Malacanthus plumieri</i>	<i>Halichoeres bivittatus</i>	<i>Ariomma melanum</i>	
		<i>Paralepidae</i>	
		<i>Uraspis secunda</i>	
		<i>Parablennius marmoreus</i>	
		<i>Chasmodes bosquianus</i>	
		<i>Hypoleurochilus geminatus</i>	
		<i>Hypsoblennius henz</i>	

Table 14.4, continued.

Pleuronectiformes	Elasmobranchs	Scorpaeniformes	Gadiformes
<i>Ancylopsetta dilecta</i>	<i>Narcine brasiliensis</i>	<i>Neomerinthe hemingwayi</i>	<i>Laemonema barbatulum</i>
<i>Ancylopsetta quadrocellata</i>	<i>Raja ackleyi</i>	<i>Pontinus rathbuni</i>	<i>Ophidion beani</i>
<i>Bothus lunatus</i>	<i>Dipturus olseni</i>	<i>Scorpaena agassizi</i>	<i>Ophidion selenops</i>
<i>Bothus ocellatus</i>	<i>Bathyraja spinicauda</i>	<i>Scorpaena brasiliensis</i>	
<i>Chascanopsetta lugubris</i>	<i>Raja texana</i>	<i>Scorpaena calcarata</i>	
<i>Citharichthys arenaceus</i>	<i>Dasyatis sabina</i>	<i>Scorpaena dispar</i>	
<i>Citharichthys cornutus</i>	<i>Dasyatis violacea</i>	<i>Scorpaena grandicornis</i>	
<i>Citharichthys macrops</i>	<i>Gymnura altavela</i>	<i>Scorpaena plumieri</i>	
<i>Citharichthys spilopterus</i>	<i>Gymnura micrura</i>	<i>Scorpaenidae</i>	
<i>Cyclopsetta fimbriata</i>	<i>Urolophus jamaicensis</i>	<i>Bellator brachychir</i>	
<i>Engyophrys senta</i>	<i>Myliobatis goodei</i>	<i>Bellator egretta</i>	
<i>Etropus crossotus</i>	<i>Squalidae</i>	<i>Bellator militaris</i>	
<i>Etropus rimosus</i>	<i>Etmopterus gracilispinis</i>	<i>Peristedion gracile</i>	
<i>Gastropsetta frontalis</i>	<i>Etmopterus hillianus</i>	<i>Prionotus alatus</i>	
<i>Paralichthys albigutta</i>	<i>Centroscyrnus coelolepis</i>	<i>Prionotus ophryas</i>	
<i>Paralichthys lethostigma</i>	<i>Breviraja plutonia</i>	<i>Prionotus roseus</i>	
<i>Paralichthys squamilentus</i>	<i>Alopias vulpinus</i>	<i>Prionotus longispinosus</i>	
<i>Syacium gunteri</i>	<i>Alopias superciliosus</i>	<i>Prionotus rubio</i>	
<i>Syacium micrurum</i>	<i>Isurus paucus</i>	<i>Prionotus scitulus</i>	
<i>Syacium papillosum</i>	<i>Carcharhinus isodon</i>	<i>Prionotus tribulus</i>	
<i>Etropus sp</i>	<i>Carcharhinus altimus</i>	<i>Myoxocephalus quadricornis</i>	
<i>Bothidae</i>	<i>Carcharhinus longimanus</i>	<i>Prionotus stearnsi</i>	
<i>Paralichthys sp.</i>	<i>Carcharhinus brevipinna</i>	<i>Trachyscorpia cristulata</i>	
<i>Citharichthys sp.</i>	<i>Carcharhinus porosus</i>		
<i>Bothus robinsi</i>	<i>Carcharhinus perezii</i>		
<i>Pleuronectiformes</i>	<i>Carcharhinus signatus</i>		
<i>Citharichthys gymnorhinus</i>	<i>Mustelus norrisi</i>		
<i>Pleuronectidae</i>	<i>Triakis semifasciata</i>		
<i>Gymnachirus melas</i>	<i>Sphyrna media</i>		
<i>Symphurus civitatus</i>			
<i>Symphurus diomedianus</i>			
<i>Symphurus minor</i>			
<i>Symphurus marginatus</i>			
<i>Symphurus plagiusa</i>			
<i>Symphurus pusillus</i>			
<i>Symphurus urospilus</i>			
			Others
			<i>Xenolepidichthys dalgleishi</i>
			<i>Engraulidae</i>
			<i>Synodontidae</i>
			<i>Argentina striata</i>
			<i>Anchoa lyolepis</i>
			<i>Chaunax stigmaeus</i>
			<i>Gymnothorax saxicola</i>
			<i>Harengula jaguana</i>
			<i>Echiopis punctifer</i>
			<i>Gobiesox strumosus</i>
			<i>Ogcocephalus radiatus</i>

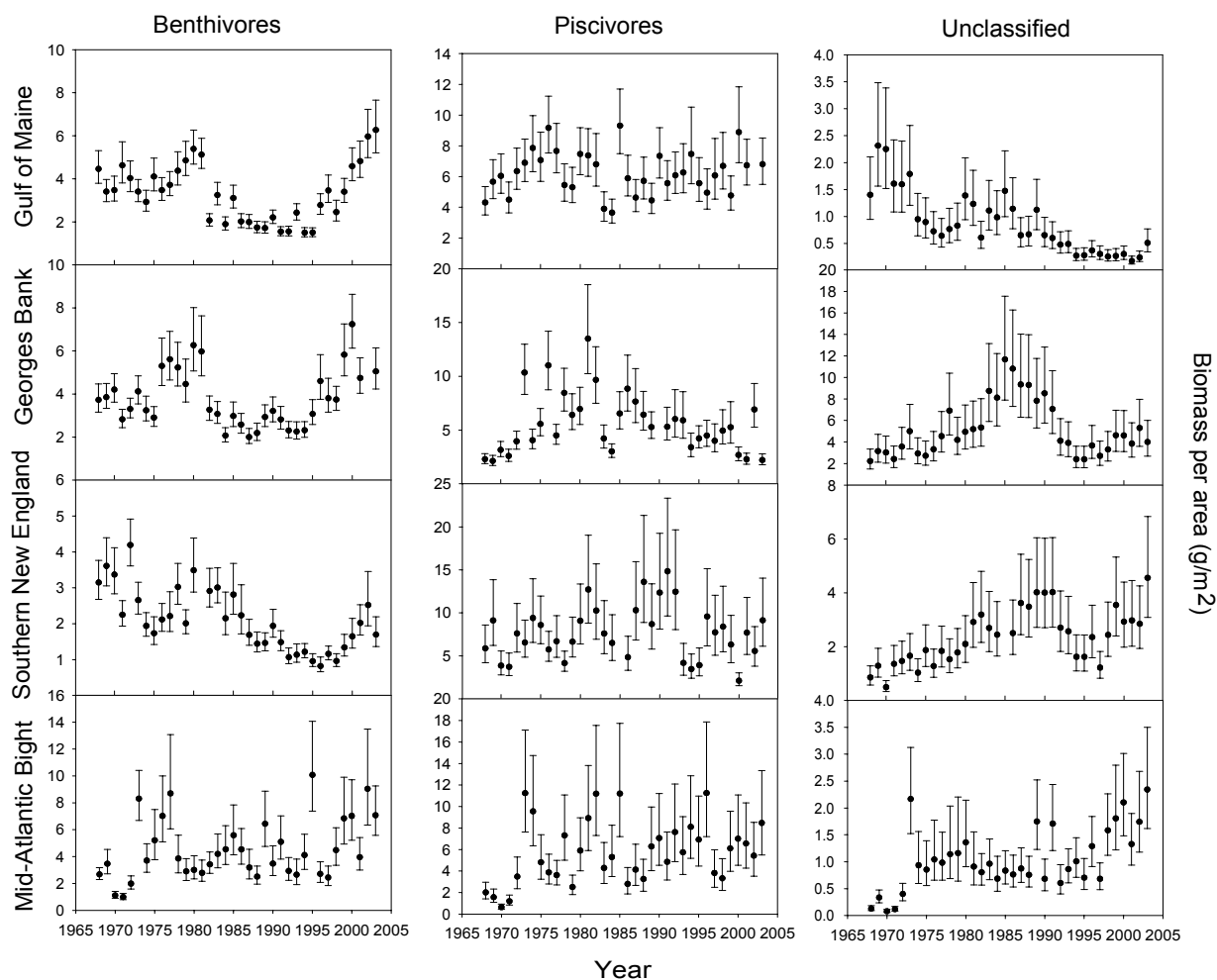


Figure 14.1. Time series of annual demersal biomass production (g m^{-2}) by benthivores, piscivores, and unclassified species in four regions of the Northeast United States Continental Shelf Ecosystem (Gulf of Maine, Georges Bank, Southern New England, and Mid-Atlantic Bight) during 1968-2003.

15. Large Pelagics (coastal sharks, pelagic sharks, and highly migratory species)

William J. Overholtz (nodes #25-27)

Background and Estimation Approaches

Bluefin tuna Virtual Population Analysis (VPA) estimates of stock size and biomass were obtained from a recent ICCAT (International Commission for the Conservation of Atlantic Tunas) stock assessment (ICCAT 2003). For bluefin tuna we assumed that 50% of the age 3+ VPA biomass occupies the New England region during July-October. This approach produced a biomass of 9,067 mt during July-October and an annual average biomass of 3,022 for the entire region (Table 15.1). Combining subjective information about the distribution of bluefin tuna during their residency period from the Mid-Atlantic region to the Gulf of Maine with some information in the literature (Chase 2002), we assumed that 45% of the regional contingent was found in both the Gulf of Maine and Georges Bank ecoregions and 10% in the SNE region. Biomass in the 4 ecoregions was the product of the regional proportions and the average annual biomass (Table 15.1).

Since no stock abundance information is available for yellowfin, bigeye, albacore, swordfish, and white-blue marlin, we developed a ratio method with Japanese longline ICCAT data (1978-1988, 5,640 sets) for the United States Exclusive Economic Zone (US EEZ) (Hoey *et al.* 2002). We used the ratio between catch rates for these species and bluefin tuna from Hoey *et al.* (2002) to produce a raising factor to scale tuna-billfish numbers during 1996-2000 to bluefin tuna numbers for the same period. We used ICCAT SCRS reports for each species to obtain mean weight data, and this was used to estimate biomass during each year. An assumption concerning the relative proportion of each stock in the 4 ecoregions was also made with distribution maps available in the ICCAT SCRS reports for each species. Average biomass for the 1996-2000 period was calculated for bluefin tuna, yellowfin tuna, bigeye tuna, albacore tuna, swordfish, and a white-blue marlin aggregate group.

Annual production for bluefin and bigeye tuna was calculated from VPA results for these species obtained from ICCAT SCRS Reports. Production data for these two species were used to calculate P:B ratios (bluefin tuna = 0.316, bigeye = 0.558). Production for albacore was calculated from the P:B ratio for bluefin tuna and yellowfin by using the P:B ratio for bigeye tuna. We assumed that swordfish and white-blue marlin are less productive, so a P:B ratio of 0.2 was used for these species. Consumption was calculated by assuming that the daily ration for the tunas was the same as for bluefin tuna (3%) and multiplying this value by the biomass during 1996-2000. Swordfish and white-blue marlin were assumed to have a daily ration of 1% body weight (BW). Landings for these species were obtained from ICCAT SCRS Reports, and it was assumed that only 10% of the average landings during 1996-2000 occurred on the continental shelf for albacore, yellowfin, bigeye, swordfish, and white-blue marlin (5% for yellowfin tuna) (Table 15.2). United States Bluefin tuna landings were averaged for 1996-2000 and scaled to account for residency time (Table 15.2). Data for all the tuna and billfish were summed for each ecoregion for biomass, production, consumption, and landings and converted to g m^{-2} (Table 15.3).

To estimate blue shark abundance, we used the ratio between blue shark and bluefin tuna catch rates from Hoey *et al.* (2002) to produce a raising factor to scale blue shark numbers during 1996-2000 to bluefin tuna numbers for the same period. This exercise produced a ratio of 1.5. Next a weighted average mean weight (drawn) was calculated from recreational mean weight

data (24.59 kg) collected during MRFSS interviews and a factor of 1.96 round:drawn ratio was used to convert to round weight (48.19 kg) (Cortez 2002). Biomass in the region was estimated by assuming that 50% of the stock (Kohler 1988) is found in the SNE-GOM area during May-October. This yielded a calculated biomass of 7,950 mt for the six month period and an annual average of 3,975 mt (Table 15.4). We further assumed that the biomass was equally distributed (Kohler 1988) over the SNE-GOM ecoregions, with 1,325 mt in each region (Table 15.4).

For the other sharks (hammerhead, shortfin mako, thresher, dusky, porbeagle, sandbar, and other) we used the ratio between the catch rates of these sharks and blue shark from Hoey *et al.* (2002) to produce a raising factor to scale numbers during 1996-2000 to blue shark numbers for the same period. Next a weighted average mean weight (drawn) was calculated from recreational mean weight data collected during MRFSS interviews for blue, mako, thresher, and porbeagle shark. The average weight for mako shark was used for sandbar and dusky, while the average weight for blue shark was used for hammerhead shark because no information for these species was available. A factor of 1.96 round:drawn ratio was used to convert to round weight for each species (Cortez 2002). We further assumed that the biomass was unequally distributed over the MA-GOM ecoregions on a seasonal basis.

Production and Consumption

Consumption by sharks in the four regions was estimated from daily ration estimates for blue (0.056) and mako (0.010) shark available from the literature (Stillwell and Kohler 1982; Kohler 1988). An average of these two values (0.008) was used to estimate consumption for the other shark species. Production for all sharks was estimated by assuming a P:B ratio of 0.1. This ratio was used with average biomass to calculate production for each species. Recreational and commercial landings of sharks were averaged during 1996-2000, scaled down to account for the percentage landed in the region, and scaled to an annual basis since sharks are only present during about half the year. Data for biomass, production, consumption, and landings were further scaled to g m^{-2} for each ecoregion and combined into a pelagic group (thresher, mako, blue, porbeagle, and hammerhead) and a coastal group (dusky, sandbar, other) (Table 15.5).

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Table 15.1. Bluefin tuna biomass, average biomass, and regional average biomass during 1996-2000 (mt).

Bluefin tuna biomass in NE region Jul–Oct		9067 (4 month residency)
Annual average biomass		3022
Region	% Annual average biomass	Biomass
GOM	0.45	1359.9
GB	0.45	1359.9
SNE	0.1	302.2
MA	0	0

Table 15.2. Average landings adjusted for seasonality for tuna, billfish and sharks during 1996-2000.

Species	Average Landings 1996-2000 (mt)
Bluefin tuna	316.65
Bigeye	10.20
Yellowfin	92.60
Albacore	14.40
Swordfish	0.58
White-blue marlin	1.28
Blue shark	56.96
Shortfin mako	82.57
Thresher	47.45
Porbeagle	2.18
Dusky	104.64
Sandbar	698.33
Hammerhead	NA
Other	NA

Table 15.3. Average biomass (B), consumption (C), production (P), and landings (L) in g m^{-2} for tuna and billfish by ecoregion during 1996-2000.

Tuna, billfish		$\text{g m}^{-2} \text{ yr}^{-1}$		
area	B	C	P	L
GOM	0.018341	0.07219	0.012875	0.001801
GB	0.035163	0.137283	0.024003	0.003406
SNE	0.009904	0.041785	0.005782	0.001071
MA	0.008747	0.042862	0.004366	0.001268

Table 15.4. Blue shark biomass, average biomass, and regional average biomass during 1996-2000.

Blue shark biomass in NE region May–Oct		7950 (6 month residency)
Annual average biomass		3975
Region	% Annual average biomass	Biomass
GOM	0.3333	1324.868
GB	0.3333	1324.868
SNE	0.3333	1324.868
MA	0	0

Table 15.5. Average biomass (B), consumption (C), production (P), and landings (L) in g m^{-2} for pelagic and coastal sharks by ecoregion during 1996-2000.

Pelagic sharks		$\text{g m}^{-2} \text{yr}^{-1}$		
Area	B	C	P	L
GOM	0.013014	0.013513	0.001301	0.00023
GB	0.024358	0.025903	0.002436	0.000794
SNE	0.019873	0.022623	0.001987	0.001153
MA	0.010237	0.012939	0.001024	0.001044

Coastal sharks		$\text{g m}^{-2} \text{yr}^{-1}$		
Area	B	C	P	L
GOM	0	0	0	0
GB	0	0	0	0
SNE	0.015858	0.023153	0.001586	0.005451
MA	0.016986	0.024799	0.001699	0.005838

16. Pinnipeds

Debra L. Palka and Gordon T. Waring (node #28)

Background

Seals found in the EMAX study ecoregions include the harbor seal (*Phoca vitulina*), gray seal (*Halichoerus grypus*), harp seal (*Pagophilus groenlandicus*), and hooded seal (*Cystophora cristata*). Harbor seals are year-round inhabitants of the coastal waters of eastern Canada and Maine (Burns 2002) and occur seasonally along the southern New England and New York coasts from September through late May (Waring *et al.* 2004). Gray seals found in the U.S. Atlantic are part of the western North Atlantic population (Hall 2002) that inhabit waters from New England to Labrador and are centered in the Sable Island region of Nova Scotia. However, some pupping has been observed on several isolated islands along the Maine coast and in Nantucket-Vineyard Sound, Massachusetts (Waring *et al.* 2004). Harp seals are the most abundant pinniped in the northern Atlantic and Arctic Oceans (Lavigne 2002; Stenson *et al.* 2003); however, over the past decade during January to May, numbers of sightings and strandings have been increasing off the east coast of the U.S. from Maine to New Jersey (Waring *et al.* 2004). Hooded seals occur throughout much of the northern North Atlantic and Arctic Oceans, preferring deeper water and occurring farther offshore than harp seals (Kovacs 2002). Hooded seals tend to wander and have been seen in New England waters during January to May and as far south as Puerto Rico during summer and autumn (Mignucci-Giannoni and Odell 2001; Waring *et al.* 2004).

Data Sources and Quantitative Approach for Biomass Estimates

Biomass (in metric tons) of pinnipeds within an ecoregion was calculated as the sum of the seasonally averaged biomass of each species within that region. Biomass per area (in g m⁻²) was calculated as biomass (in metric tons) per area of the ecoregion (in km²; Table 1.1). The seasonally averaged biomass of species *k* within ecoregion *i* was calculated as the average of the seasonal biomass estimates for species *k* in ecoregion *i*:

$$(EQ. 16.1) \quad Average\ Biomass_{ki} = \frac{\sum_{season} (seasonal\ biomass_{ki})}{4}.$$

The seasonal biomass estimate for species *k* within ecoregion *i* was the sum of the seasonal biomass of females and the seasonal biomass of males over all seasons *l*:

$$(EQ. 16.2) \quad Seasonal\ biomass_{ki} = \sum_{season\ l} \sum_{sex\ j} \%sex_{kj} \bullet total\ seasonal\ abundance_{kli} \bullet avg\ weight\ of\ sex_{kji}$$

The seasons were defined as summer (June to August), fall (September to November), winter (December to February), and spring (March to May). The approaches used to estimate the seasonal abundance of each species and the animal weight for each sex of each species is described below.

Harbor seal abundance estimates were based on 2000-2001 aerial surveys (Barlas 1999; Hoover *et al.* 1999; Slocum *et al.* 1999; deHart 2002; Gilbert *et al.* 2005), and other ancillary data. Sexual parity was assumed based on literature review for other regions. The population

age structure was assumed to be 30% ages 1-3 and 70% ages 4+. Age 7 mean weights (kg) for males (80.791) and females (68.796) (M. Hammill, pers. comm., DFO, Mont-Joli, Quebec) were used to estimate Gulf of Maine biomass. Age 6 weights (76.450 males, 66.023 females) were used for the Southern New England and Mid-Atlantic Bight regions.

Gray seal abundance estimates were derived from 2000-2003 surveys (Barlas 1999; S. Wood pers. comm., UMass Boston) and other ancillary data. A 50:50 sex ratio was assumed. Age 9 weights (kg) for males (208.0) and females (153.0) (Mohn and Bowen 1996) were used to estimate biomass in all ecoregions.

Harp seal abundance estimates were based on strandings and bycatch data (Waring *et al.* 2004). A 50:50 sex ratio was assumed. Juvenile harp seals comprise the bycatch and strandings data; therefore, age 4 weights (kg) were used to estimate biomass. Female and male age 4 weights were derived from the following equations (Chabot *et al.* 1996):

$$(EQ. 16.3) \quad \text{Female: mass} = (98.6 e^{(-1.325 e^{-0.383 \cdot \text{age}})});$$

$$(EQ. 16.4) \quad \text{Male: mass} = (103.3 e^{(-1.326 e^{-0.352 \cdot \text{age}})}).$$

Hooded seal abundance estimates were based on strandings and bycatch data (Waring *et al.* 2004). The stranding network saw primarily juvenile hooded seals (at ~ 120 cm / 27 kg with about 6-12 adults a year at ~215 cm / 136 kg; B. Rubinstein, pers. comm., New England Aquarium). Most were under 14 months because they were bluebacks, which have a distinct coloration until they molt at 14 months of age. Mean weight was calculated as $(0.95 * 27 \text{ kg} + 0.05 * 136 \text{ kg}) = 32.45 \text{ kg}$.

Quantitative Approach for Production Estimates

Net production biomass (in metric tons) within an ecoregion was calculated as the sum of the net production of species found in that ecoregion. Net production biomass per area (in g m^{-2}) was calculated as biomass (in metric tons) per area of the ecoregion (in km^2 ; Table 1.1). Net production biomass of species k within ecoregion i was calculated as the product of the seasonally-averaged biomass of species k within ecoregion i (eq. 16.1) and the net production rate for species k :

$$(EQ. 16.5) \quad \text{net production biomass}_{ki} = (\text{seasonal avg biomass}_{ki} \bullet \text{net production rate}_k) / 1000.$$

The net production rate of harbor seals was assumed to be 6.5%, which is the percentage the harbor seal population in Maine increased between 1981 and 2001 (J. Gilbert, pers. comm.). In general, a net maximum production rate of 12% has been recognized as a default value for pinnipeds. This is based on theoretical modeling showing that pinniped populations may not grow at rates much greater than 12% given the constraints of their reproductive history (Barlow *et al.* 1995). Because the number of breeding gray seals in U.S. waters is expanding, a 12% net production rate was assumed. This is comparable to the rate of increase observed on Sable Island (Lesage and Hammill 2001). However, for both harp and hooded seals, a 6.5% value was assumed because these populations are not breeding in U.S. waters and the animals found in U.S. waters are essentially stragglers at the outskirts of their range.

Quantitative Approach for Consumption Estimates

Consumption biomass (in metric tons) within an ecoregion was calculated as the sum of the annual consumption biomass of species found in that region. Consumption biomass per area (in g m^{-2}) was calculated as consumption biomass (in metric tons) per area of the ecoregion (in km^2 ; Table 1.1). The annual consumption biomass (in metric ton) for species k within ecoregion i was estimated by:

$$(EQ. 16.6) \quad \text{Consumption biomass}_{ik} = \frac{\sum_{\text{season } s} \sum_{\text{days in } s} \text{daily feeding rate}_{ks} \cdot (\text{biomass / day})_{iks}}{1000},$$

where the $(\text{daily feeding rate})_{ks}$ (in kg day^{-1}) is the daily feeding rate of species k for season s and the $(\text{biomass day}^{-1})_{iks}$ (in kg) is the biomass of species k within ecoregion i and within season s . The feeding rate per individual per day is defined as a percentage of its biomass. There is an inverse relation between feeding rate and body weight (Sargeant 1969). The daily feeding rate of pinnipeds was estimated using Innes *et al.* (1987):

$$(EQ. 16.7) \quad \text{Daily feeding rate}_i = \frac{0.068 \cdot \text{avg wt}_i^{0.78}}{\text{avg wt}_i}.$$

The average body weights (avg wt) for each species are in the biomass section above.

Example Results

Biomass Estimates

The seasonal movements of pinnipeds between and outside the EMAX ecoregions are substantial, particularly for the southern two regions (Southern New England and Mid-Atlantic Bight) (Table 16.1), where there are only a few pinnipeds found in the summer. Pinnipeds primarily inhabit the Gulf of Maine region, and rarely use the Georges Bank region (Figure 16.1). Thus, it was assumed there were no seals in the Georges Bank area. Harbor seals contribute the most biomass to the pinniped mode in these U.S. waters.

Production Estimates

The patterns of production biomass (g m^{-2}) are similar to the patterns in biomass (Figure 16.1) because production biomass is simply the product of biomass and net production rate, which was assumed to be 6.5% for all species except gray seals (12%).

Consumption Estimates

Using equation 16.7, the daily feeding rate of pinnipeds ranged from 2.2% of the grey seal's body weight to 3.2% of the hooded seal's body weight, where the daily feeding rate of harbor and harp seals was 2.6% of its body weight.

The consumption biomass per area (g m^{-2}) is the highest in the Gulf of Maine and lowest in the Georges Bank and Mid-Atlantic Bight ecoregions (Figure 16.2). Harbor seals contribute most of the biomass in this node, so harbor seals contribute the most to the consumption biomass.

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Table 16.1. Seasonal abundance estimates of each pinniped species within the EMAX ecoregions. It was assumed there were no pinnipeds in the Georges Bank ecoregion.

Species	Season	Ecoregion		
		GOM	SNE	MAB
Harbor seal	Spring	95,000	5,000	200
	Summer	100,000	0	0
	Fall	95,000	5,000	100
	Winter	90,000	10,000	300
Gray seal	Spring	1,000	4,500	5
	Summer	2,000	3,000	0
	Fall	2,000	4,500	5
	Winter	2,000	6,000	10
Harp seal	Spring	200	200	0
	Summer	0	0	0
	Fall	200	200	0
	Winter	200	200	0
Hooded seal	Spring	25	25	0
	Summer	0	0	0
	Fall	25	25	0
	Winter	50	50	0

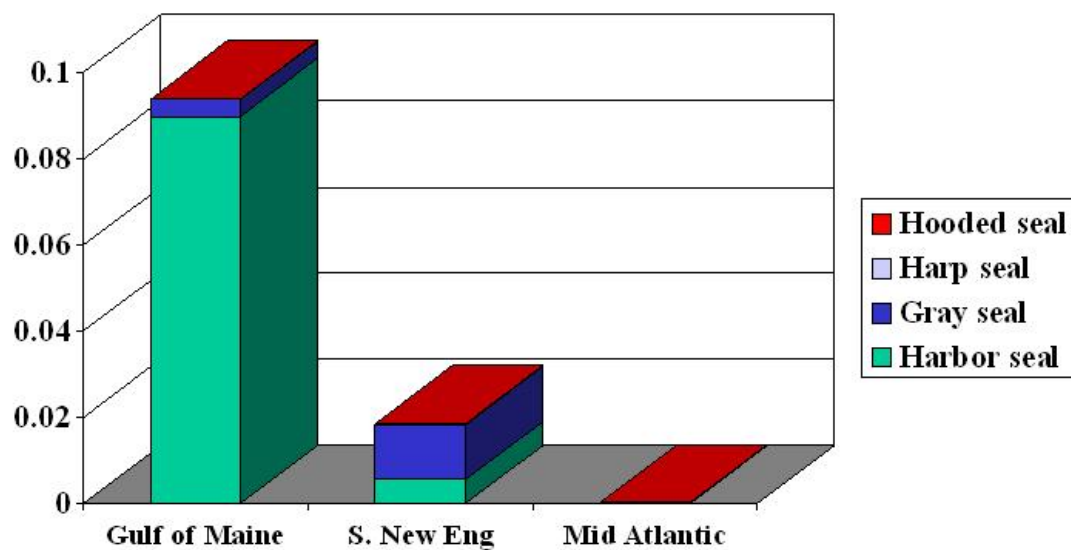


Figure 16.1. Biomass per area (in g m⁻²) of species that make up the pinniped node for each ecoregion.

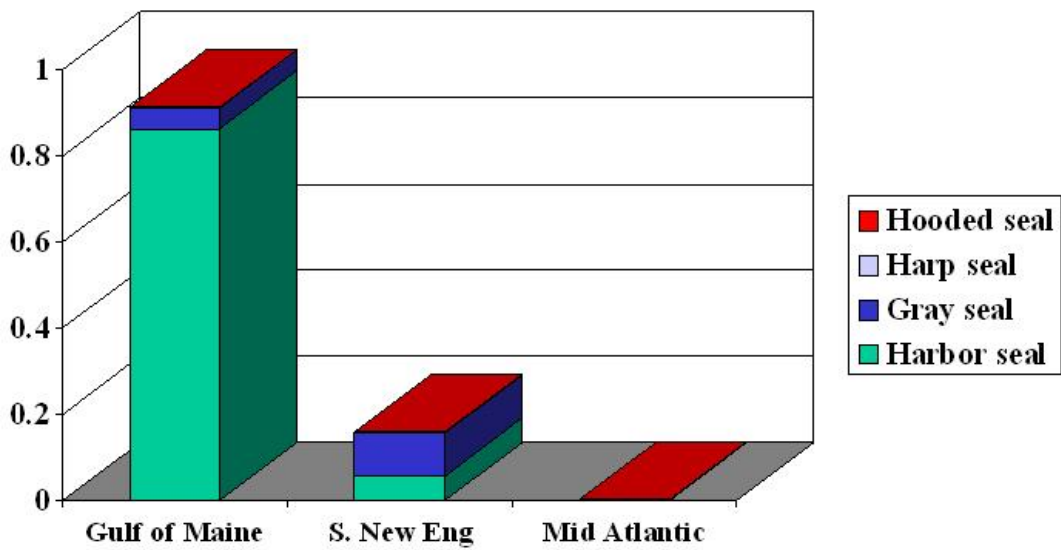


Figure 16.2. Consumption biomass per area (in g m⁻²) of species that make up the pinniped node for each ecoregion.

17. Baleen Whales and Odontocetes

Debra L. Palka (nodes #29 and 30)

Background

Cetaceans (whales, dolphins and porpoises) inhabiting the EMAX study ecoregions migrate between the four regions and also go outside them. A general description of the distribution and habit of cetaceans in the North Atlantic is found in Waring and Palka (2002). More detailed descriptions for each species are found in Waring *et al.* (2004). Cetaceans that have teeth (odontocetes) that utilize at least one of the EMAX ecoregions for some part of the year include: bottlenose dolphins (*Tursiops truncatus*), common dolphins (*Delphinus delphis*), beaked whales (*Ziphius* or *Mesoplodon* spp.), Risso's dolphins (*Grampus griseus*), harbor porpoise (*Phocena phocena*), dwarf sperm or pygmy sperm whale (*Kogia* spp.), long-fin and short-fin pilot whales (*Globicephala* spp.), sperm whales (*Physeter macrocephalus*), spotted dolphins (*Stenella frontalis*), striped dolphins (*S. coeruleoalba*), and white-sided dolphins (*Lagenorhynchus acutus*). Cetaceans with baleen that utilize some part of the EMAX ecoregions for some part of the year include: fin whales (*Balaenoptera physalus*), sei whales (*B. borealis*), humpback whales (*Megaptera novaeangliae*), minke whales (*B. acutorostrata*), and right whales (*Eubalaena glacialis*).

Data Sources

The biomass data are based on abundance shipboard and aerial sighting surveys conducted by the NMFS/NEFSC during the summers of 1998 and 1999. The 1999 survey was used to estimate abundance within the Gulf of Maine ecoregion, while the 1998 survey covered the other ecoregions (Figure 17.1). The 1998 shipboard survey was conducted from 6 July to 6 September, and two teams of observers searched for marine mammals using line transect field data collection methods. These data were analyzed using the direct duplicate line transect analysis method (Palka 1995; Palka 2005a). The 1998 aerial survey was conducted from 18 July to 21 August using standard 1-team line transect methods (Palka 2005b). The 1999 shipboard and aerial surveys were conducted during 28 July to 31 August using methods similar to those used in the 1998 surveys (Palka 2000).

Quantitative Approach for Biomass Estimates

Biomass (in metric tons) of baleen whales and odontocetes within an ecoregion was calculated as the sum of the seasonally averaged biomass of each baleen or odontocetes species within that ecoregion. Biomass per area (in g m⁻²) was calculated as biomass (in metric tons) per area of the region (in km²; Table 1.1). The seasonally averaged biomass of species *k* within ecoregion *i* was calculated as the product of the seasonal average abundance estimate for species *k* in ecoregion *i* and the average weight (in kg; Table 17.1) of an individual of species *k*:

$$(EQ. 17.1) \quad \text{Average Biomass}_{ki} = \frac{\sum_{\text{season}} (\text{seasonal abundance}_{ki})}{4} \cdot \frac{\text{avg weight}_k}{1000}.$$

The seasonal average abundance estimate was defined as the average of the abundance for each season weighted by the length of the season. The seasons were defined as summer (June to August), fall (September to November), winter (December to February), and spring (March to May). Average weights of individuals were based on values in Trites and Pauly (1998) and Kenney *et al.* (1997).

Abundance estimates were derived from shipboard and aerial line transect surveys conducted by the NEFSC in the summers (July and August) of 1998 and 1999 (Figure 17.1). The EMAX Gulf of Maine abundance estimate was derived from the 1999 survey data and the abundance estimates for the rest of the ecoregions were derived from the 1998 data. Shipboard and aerial abundance estimates within an EMAX ecoregion were derived from the length of track lines (L), number of sightings (n), and average group size (\bar{s}) within each EMAX region and the estimates of the effective strip width (esw) and $g(0)$ derived from the entire survey. Thus, the abundance for a species k within ecoregion i on platform j (ship or plane) was:

$$(EQ. 17.2) \quad Abundance_{kij} = \frac{n_{kij} \cdot \bar{s}_{kij}}{2 \cdot L_{ij} \cdot esw_{kj} \cdot g(0)_{kj}} \cdot A_{ij},$$

where A_{ij} was the area within EMAX ecoregion i that was surveyed by platform j . The total abundance for species k within a region was the sum of the aerial and shipboard abundance estimates for that species.

Abundance estimates from these surveys represent the summer season. Since each species migrates up and down the U.S. Atlantic coast in different ways and at different times, a seasonal abundance estimate for each species within each EMAX ecoregion was calculated separately. That is, the seasonal abundance estimate within each ecoregion was defined as a proportion of the summer population within that region using expert opinion and general patterns documented in the Cetacean and Turtle Assessment Program (CETAP) (1982) and Department of Navy (2005).

Note that the estimate of $g(0)$, the probability of detecting a group on the track line, was defined as 1.0 for these aerial surveys, while $g(0)$ was estimated for the shipboard data. This means the abundance estimates presented here are negatively biased, because not all whales and dolphins were seen on the track line from an airplane flying at 600 ft altitude as was assumed when $g(0)=1$. During 2004, methods developed to estimate $g(0)$ for aerial survey data indicate $g(0)$ for large whales as about 0.2 and for smaller cetaceans about 0.6 to 0.7 (Palka 2005). Consequentially, if $g(0)$ was included in the calculation, the abundance estimates would be 50-500% higher than what is presented here, depending on the species.

Quantitative Approach for Production Estimates

Net production biomass (in metric tons) within an ecoregion was calculated as the sum of the net production of species found in that region. Net production biomass per area (in $g\ m^{-2}$) was calculated as biomass (in metric tons) per area of the ecoregion (in km^2 ; Table 1.1). Net production biomass of species k within ecoregion i was calculated as the product of the seasonally averaged biomass of species k (eq. 17.1) within ecoregion i and the net production rate for species k :

$$(EQ. 17.3) \quad net\ production\ biomass_{ki} = (seasonal\ avg\ biomass_{ki} \cdot net\ production\ rate_k) / 1000.$$

The net production rate of cetaceans is poorly understood because only a few studies have calculated a species-specific rate. However, a value of 4% is recognized as a default value for both baleen and odontocetes. This is based on theoretical modeling showing that cetacean populations may not grow at rates much greater than 4% given the constraints of their reproductive history (Barlow *et al.* 1995). Thus, 4% was used as the net production rate for all baleen and odontocetes, except if there was a species-specific estimate available. The only species-specific estimate of the net reproductive rate that was available and differed from 4% was for right whales (0%; Fujiwara and Caswell 2001).

Quantitative Approach for Consumption Estimates

Consumption biomass (in metric tons) within an EMAX region was calculated as the sum of the annual consumption biomass of species found in that region. Consumption biomass per area (in g m⁻²) was calculated as consumption biomass (in metric tons) per area of the region (in km²; Table 1.1). The annual consumption biomass (in metric ton) for species *k* within ecoregion *i* was estimated by:

$$(EQ. 17.4) \quad Consumption\ biomass_{ik} = \frac{\sum_{season\ s} \sum_{days\ in\ s} daily\ feeding\ rate_{ks} \bullet (biomass / day)_{iks}}{1000}$$

where the (daily feeding rate)_{ks} (in kg day⁻¹) is the daily feeding rate of species *k* for season *s* and the (biomass day⁻¹)_{iks} (in kg) is the biomass of species *k* within ecoregion *i* and within season *s*. The feeding rate per individual per day is defined as a percentage of its biomass.

There is an inverse relationship between feeding rate and body weight (Sargeant 1969). Thus, for large whales (baleen whales and sperm whales) the daily feeding rate (in kg day⁻¹) for species *i* was estimated using (Innes *et al.* 1987):

$$(EQ. 17.5) \quad Daily\ feeding\ rate_i = \frac{0.042 \bullet avg\ wt_i^{0.67}}{avg\ wt_i}.$$

Because baleen whales do not feed while migrating and mating in the winter, it was assumed the daily feeding rate for baleen whales in winter was 0%; all other seasons followed Equation 17.5.

The range of daily feeding rates for odontocetes is 4-11% (Table 17.2). For this study it was assumed the daily feeding rate for harbor porpoises was 8.3% of body weight, and for other odontocetes (excluding sperm whales) it was assumed to be 4.2% of body weight.

Example Results

Biomass Estimates

The seasonal distribution of baleen and odontocetes varies greatly by species (Table 17.3). Cetacean biomass per area (in g m⁻²) is dominated by baleen whales, even though there are fewer species of baleen whales than odontocetes (Figure 17.2). The cetacean biomass per area is highest in the Gulf of Maine and Georges Bank, and the lowest in the Mid-Atlantic Bight.

Among the baleen whales, the most common species are fin and humpback whales (Figure 17.2A). Within the odontocetes, most of the biomass is from pilot whales (long and short fin), common dolphins, and white-sided dolphins (Figure 17.2B). The Gulf of Maine region has the lowest number of species but the most biomass. The Georges Bank and Southern New England regions have the most diverse composition of species. Note that all the species found in the ecoregions south of the Gulf of Maine are also found offshore of the EMAX ecoregions. For some species, the abundance offshore is much greater than that estimated for the EMAX regions.

Production Estimates

Little is known about cetacean reproduction rates, so the default value of 4% annual reproduction rate was used for all species except right whales (0%). Thus the patterns of production ($\text{g m}^{-2} \text{yr}^{-1}$) are the same as those for biomass (Figure 17.2). The magnitude, however, is 4% of the biomass.

Consumption Estimates

Using equation 17.5, the daily feeding rate of baleen whales during seasons other than winter ranged from 1.2% of a fin or sei whale's body weight to 2.3% of a minke whale's body weight. It was assumed baleen whales did not eat during winter (January to March). It was also assumed the daily feeding rate of harbor porpoises was 8.3% of its body weight, odontocetes (except sperm whales) were 4.2% of their body weight, and sperm whales (using equation 17.5) was 1.6% of its body weight.

The consumption rate per area ($\text{g m}^{-2} \text{yr}^{-1}$) is the highest in the Gulf of Maine and lowest in the Mid-Atlantic Bight (Figure 17.3). Baleen whales consume more than the odontocetes. Of the odontocetes, those on Georges Bank contribute the most biomass (Figure 17.2) and the most consumption biomass (Figure 17.3).

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Table 17.1. Weights (in kg) of an average animal of each species. W. = whale, D. = Dolphin. spp. = multiple species.

Baleen	Weight	Odontocete	Weight	Odontocete	Weight
Fin/Sei W.	50,000	Beaked W. spp.	826	Pilot W. spp.	851
Humpback W.	30,408	Bottlenose D.	188	Sperm W.	18,519
Minke W.	6,566	Common D.	80	Spotted D.	66
Right W.	23,383	Grampus	224	Striped D.	116
Sei W.	16,811	Harbor porpoise	31	Whitesided D.	92
Unid W.	24,000	Kogia spp.	139	Unid D.	136

Table 17.2. Daily feeding rates from the literature for various species.

Species	Area	Daily feeding rate (% of body weight)	Source
Pilot whale	Pacific	4	Sargeant 1969
Pilot whale	S. Atlantic	4.7	Sargeant 1969
Harbor porpoise	Pacific	11	Sargeant 1969
Harbor porpoise	S. Atlantic	8.3	Sargeant 1969
Killer whale	Pacific	3.6	Sargeant 1969
False killer whale	Pacific	4.7	Sargeant 1969
Bottlenose dolphin	S. Atlantic	4.2	Sargeant 1969
Bottlenose dolphin	Atlantic	4 - 6	San Miguel 1977
Bottlenose dolphin	Captive	5.2	Cheal & Gales 1991
Dall's porpoise	Japan	5.04	Ohizumi & Miyazaki 1998

Table 17.3. Seasonally-weighted average abundance estimates of cetacean species found in the EMAX regions. A. Baleen whales. B. Odontocetes. W. indicates whale, D. indicates dolphin. Spp. indicates species group.

A. Baleen whales.

Species	Region	Summer Abundance Estimate	% of Population in Region by Season				Seasonally Weighted Average Abundance
			Winter	Spring	Summer	Fall	
Fin or Sei W.	GB	183.96	0.2	1.3	1	0.4	133.37
	GOM	1343.82	0.1	0.9	1	0.7	907.08
	MAB	78.82	0.21	1	1	0.2	47.29
	SNE	463.05	0.1	0.8	1	0.3	254.68
Humpback W.	GB	100.14	0.1	1.2	1	0.2	62.59
	GOM	516.38	0.1	1	1	0.3	309.83
	MAB	100.00	0.2	1	0	1	55.00
	SNE	100.00	0.1	1	0	1	52.50
Minke W.	GB	64.17	0	1.3	1	0.1	38.50
	GOM	753.25	0.05	0.8	1	0.2	386.04
	MAB	100.00	0	2	1	0	75.00
	SNE	117.18	0	1.5	1	0.1	76.17
Right W.	GB	325.00	0.2	0.4	0.2	0.3	89.38
	GOM	325.00	0	0.1	0.7	0.5	105.63
	MAB	325.00	0.3	0.3	0.1	0.1	65.00
	SNE	325.00	0	0.2	0	0.1	24.38
Sei W.	GB	350.00	1	1	0.5	1	306.25
	GOM	350.00	0.5	1	0.5	0.5	218.75
	MAB	350.00	1	1	0	0.5	218.75
	SNE	350.00	0.2	0.5	0	0.1	70.00
Unid W.	GB	136.77	0.2	0.7	1	0.7	88.9
	GOM	369.21	0.1	0.5	1	0.5	193.84
	SNE	98.82	0.2	0.7	1	0.7	64.23

B. Odontocetes whales.

Species	Region	Summer Abundance Estimate	% of Population in Region by Season				Seasonally weighted average abundance
			Winter	Spring	Summer	Fall	
Beaked spp. W.	GB	88.62	1	1	1	1	88.62
Bottlenose D.	GB	741.95	0.05	1	1	0.2	417.34
	MAB	8491.67	0.05	1	1	0.7	5838.03
	SNE	6232.96	0.05	1	1	0.5	3817.69
Common D.	GB	10739.24	2	1.5	1	2	17451.27
	GOM	9369.25	0.7	0.7	1	1.5	9135.02
	MAB	2634.32	2	2	1	0.2	3424.62
	SNE	5862.25	2	2	1	2	10258.93
Risso D.	GB	2295.93	0	0.4	1	0.2	918.37
	MAB	1312.10	0.1	0.8	1	0.3	721.55
	SNE	3730.70	0	0.6	1	0.1	1585.55
Harbor P.	GB	30607.50	0.05	0.6	0	0.3	7269.28
	GOM	30607.5	0.4	0.4	0	0.3	8417.06
	MAB	30607.50	0.4	0.4	0	0.3	8417.06
	SNE	30607.50	0.3	0.4	0	0.3	7651.88
Kogia spp. W.	GB	25.36	0	0	1	0.5	9.51
	SNE	14.94	0	0	1	0.5	5.6
Pilot spp W.	GB	2488.99	0.1	2	1	0.3	2115.39
	GOM	2610.00	0.1	0.8	1	0.5	1566.00
	MAB	174.68	0.3	1	1	1	144.11
	SNE	1076.31	0.1	2	1	0.3	914.86
Sperm W.	GB	74.79	0.2	1	1	0.5	50.48
	SNE	12.59	0.1	1	1	0.5	8.19
Spotted D.	GB	1152.90	0	1	1	0.5	62.50
	MAB	100.00	0	1	0.5	1	62.50
Striped D.	GB	1526.79	0	0.7	1	0.2	725.23
	MAB	100.00	2	3	0	1	150.00
	SNE	13.04	0	1	1	1	9.78
Unid D.	GB	4769.9	0.1	0.7	1	0.7	2981.79
	GOM	2011.22	0.1	0.5	1	0.5	1055.89
	MAB	251.94	0.2	1	1	1	201.55
	SNE	6056.97	0.2	0.7	1	0.7	3937.03
Whiteside D.	GB	709.99	0.3	2	1	1	763.24
	GOM	20767.04	0.2	0.7	1	0.7	13498.58
	SNE	1317.21	0	2	1	0.5	1152.56

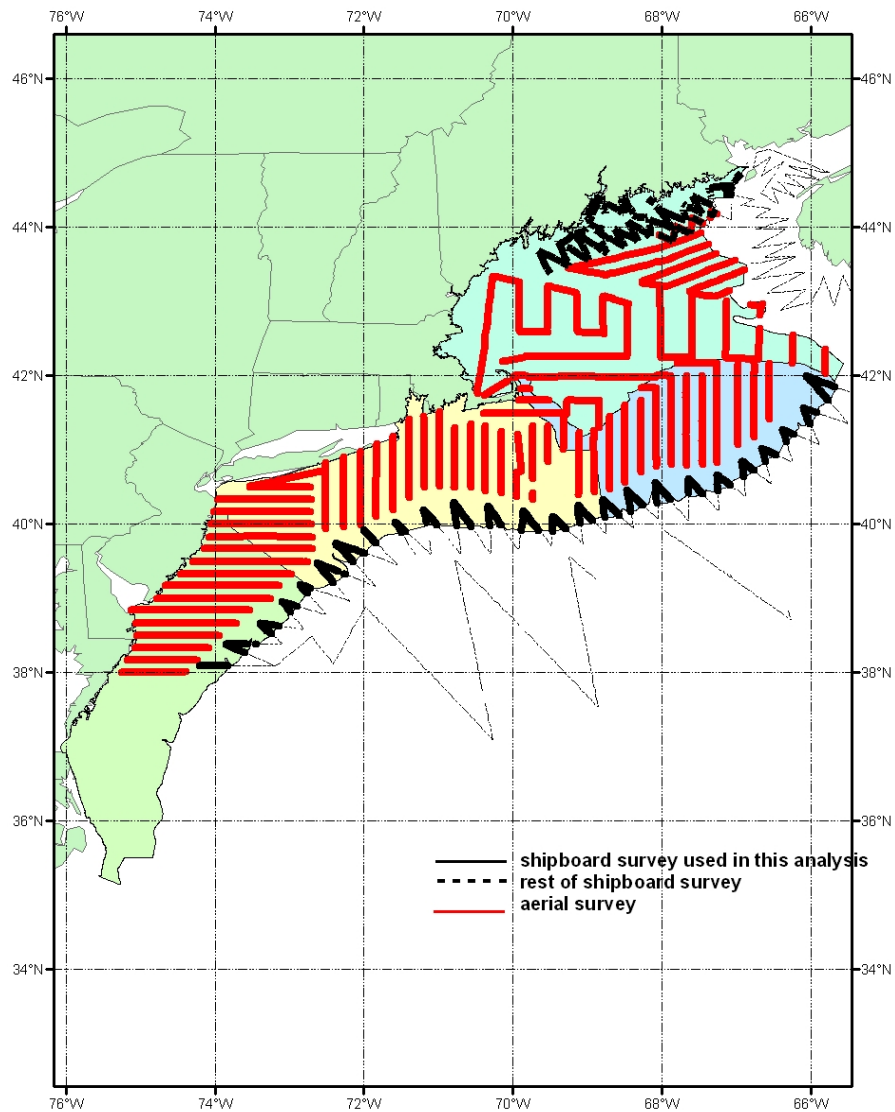
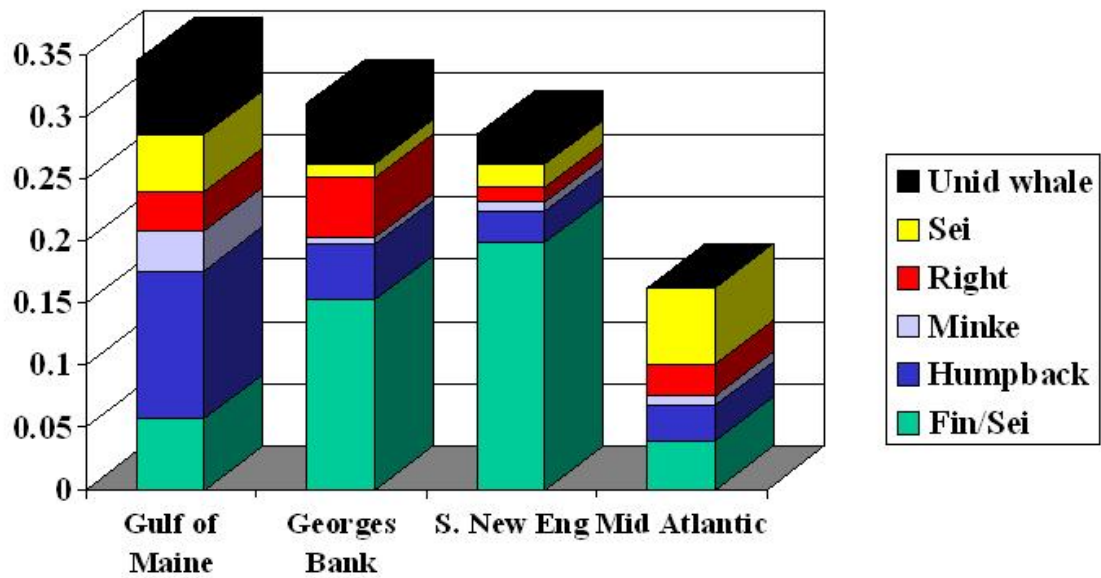


Figure 17.1. Shipboard and aerial track lines from the 1998 and 1999 marine mammal abundance surveys used to estimate abundance within the four EMAX ecoregions. Abundance from the Gulf of Maine ecoregion used 1999 data, while the other regions used 1998 data. Black track lines are from shipboard surveys, red track lines are from aerial surveys, and light gray track lines are track lines conducted in the surveys but are not part of the EMAX ecoregions.

A. Baleen



B. Odontocetes

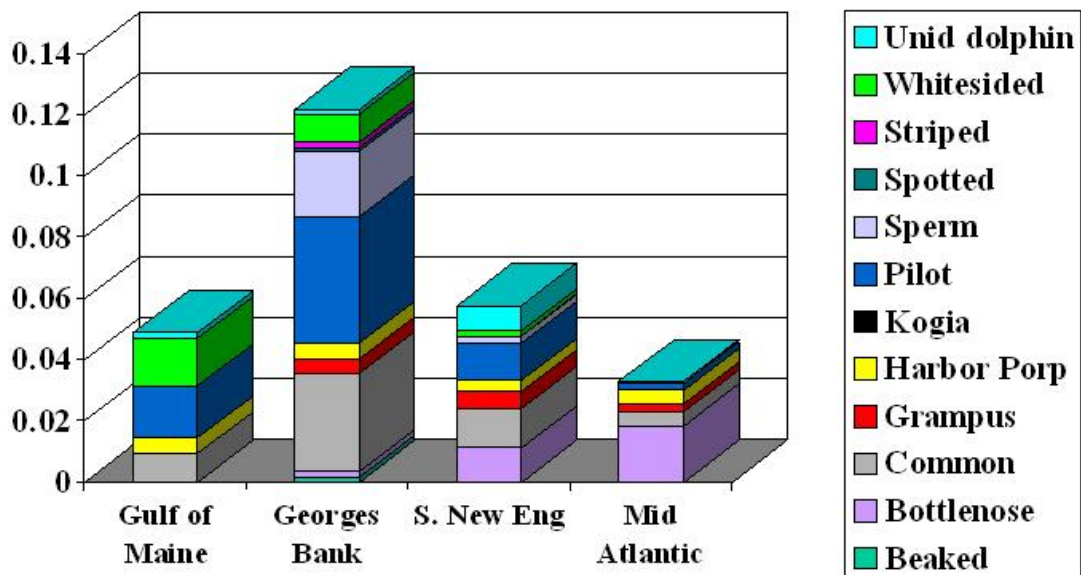
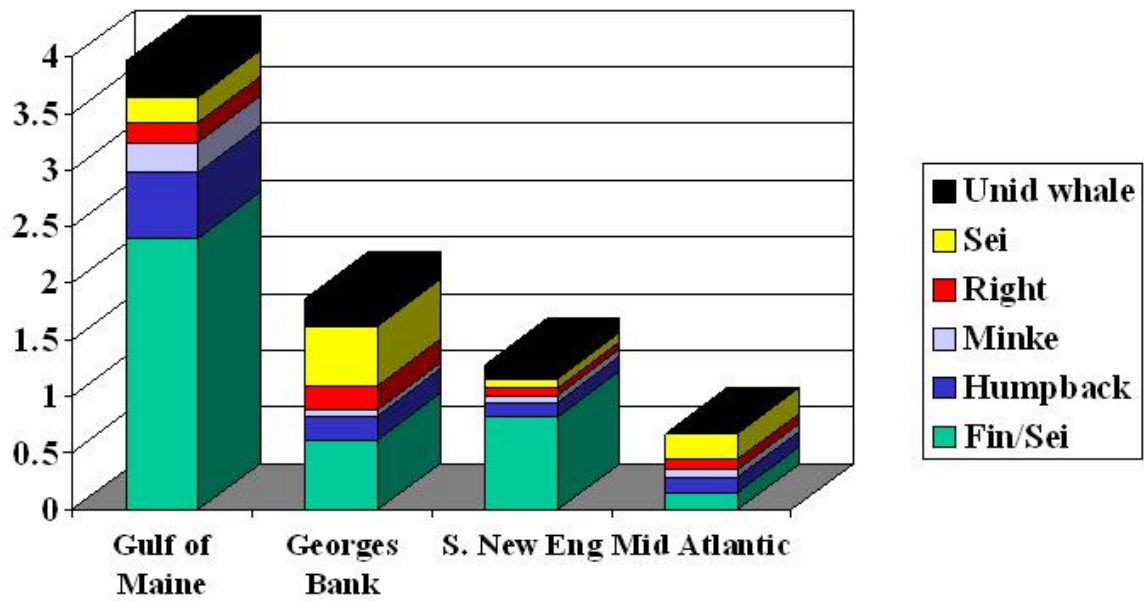


Figure 17.2. For each region, biomass per area (in g m⁻²) of species that make up the baleen (A) and odontocetes (B) nodes.

A. Baleen



B. Odontocetes

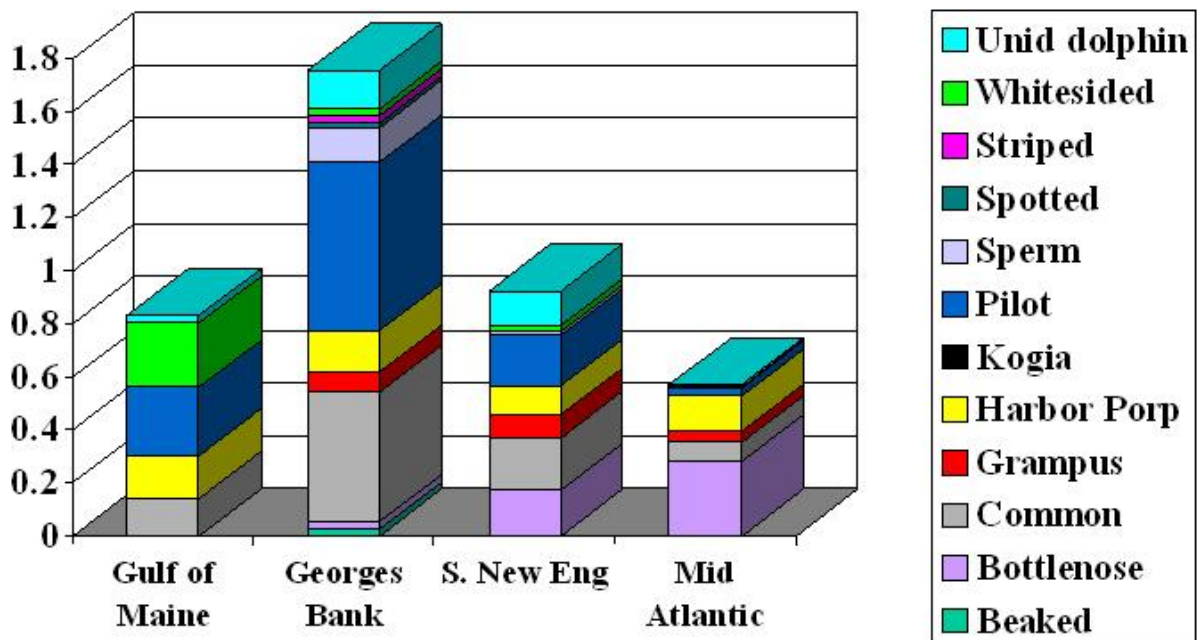


Figure 17.3. For each region, consumption biomass per area (in g m⁻²) of species that make up the baleen (A) and odontocetes (B) nodes. The daily feeding rates of odontocetes was assumed to be 4.2% of the biomass for all species except harbor porpoises, which was assumed to be 8.3%.

18. Seabirds

William J. Overholtz (node #31)

Background and Estimation Approaches

Marine birds are represented by 20 species in the Northeast U.S. Continental Shelf Ecosystem and are moderately abundant, especially on Georges Bank (Schneider and Heinemann 1996). There have been no large scale surveys of marine bird populations conducted in the region since 1988. The region is generally thought of as a seasonal feeding area with few species actually nesting locally. Eleven species were chosen as important offshore predators to include in the energy budgets of the four EMAX ecoregions (Table 18.1).

Schneider and Heinemann (1996) provide the mean and standard deviation for various seabirds during 1978-1988 as well as abundance data (deviations for the mean) for the same period. Since no current seasonal abundance data are available for the region, the information for quarterly abundance during 1978-1980 in Powers (1983; Appendix 5 in that publication) was used. These data were standardized to the highest quarterly value and used with the mean, standard deviation, and yearly deviation for each species to calculate quarterly numbers of birds during 1978-1988, assuming that the seasonal distribution of seabirds has not changed over time. Since the three species of shearwaters are similar in size and greater shearwaters are by far the most abundant, their abundance was combined.

The proportion of seabirds in each ecoregion was calculated from seasonal and regional abundance data provided in Powers (1983; Appendix 1 in that publication). Quarterly abundance by region was summed and divided by the total abundance in all regions for that species. Since there are no estimates of abundance for the 1996-2000 period, the average abundance during 1984-1988 was calculated for each quarter and converted to biomass with estimates of average species specific weight from Powers and Bachus (1987). Quarterly biomass estimates were averaged and the proportions by region used to partition biomass into the four ecoregions (Table 18.2).

Production and Consumption

Consumption by seabirds was estimated from quarterly numbers of birds and estimates of daily ration (kg day^{-1}) from an energetics equation (Innes 1987). The daily consumption by each species was estimated and expanded to a quarterly basis (91.5 days). Quarterly consumption was summed and a yearly average was calculated (Table 18.3). Production was estimated with a P:B ratio (0.275) obtained from Savonkoff *et al.* (2004) and applied to the average biomass. Quarterly estimates were summed and averaged for the year (Table 18.3). Results for all species were summed and apportioned into each ecoregion (Table 18.4)

References

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Table 18.1. Marine birds included in energy budget calculations for the four ecoregions on the Northeast U.S. Continental Shelf Ecosystem.

Greater shearwater (*Puffinus gravis*)
 Sooty shearwater (*Puffinus griseus*)
 Cory's shearwater (*Calonectris diomedae*)
 Northern gannet (*Sula bassanus*)
 Black-legged kittiwake (*Rissa triactyla*)
 Great black-backed gull (*Larus marinus*)
 Herring gull (*Larus argentatus*)
 Northern fulmar (*Fulmarus glacialis*)
 Wilson's storm petrel (*Oceanites oceanicus*)
 Red phalarope (*Phalaropus fulicarius*)
 Laughing gull (*Larus philadelphia*)

Table 18.2. Example calculation for biomass of Northern gannet by yearly quarter and region.

Northern Gannet	Quarter				
	Jan-Mar	Apr-Jun	Jul-Sep	Oct-Dec	Average
Average N (1984-1988)	219,064	238,623	1,304	113,444	143,109
Average Biomass (1984-1988) (mt)	657.2	715.9	3.9	340.3	429.4

	EMAX Regions			
	GOM	GB	SNE	MAB
Proportion of Total Study Area	0.125	0.227	0.361	0.287
Average Biomass by Region (mt)	53.7	97.4	155	123.2

Table 18.3. Quarterly consumption and average consumption and production for northern gannet during 1996-2000.

Northern Gannet	Quarter			
	Jan-Mar	Apr-Jun	Jul-Sep	Oct-Dec
Quarterly C (1996-2000) (mt)	5921.145	6449.819	35.24491	3066.307
Average Quarterly C	3868.129			

Quarterly P (1996-2000) (mt)	180.7277	196.8641	1.07576	93.59112
Average Quarterly P	118.0647			

Table 18.4. Average biomass (B), consumption (C), and production (P) ($\text{g m}^{-2} \text{ yr}^{-1}$) for seabirds by ecoregion during 1996-2000.

Area	B	C	P
GOM	0.005878	0.063031	0.001616
GB	0.014393	0.15652	0.003958
SNE	0.006334	0.064728	0.001742
MA	0.003634	0.03691	0.000999

19. Detritis - Particulate Organic Carbon (POC) and Dissolved Organic Carbon (DOC)

John E. O'Reilly and David D. Dow (nodes #35 and 36)

Background/Data Sources

Organic carbon bound in a dissolved form (DOC) represents the largest pool of organic matter in the ocean, exceeding standing stocks of particulate organic carbon (POC) and phytoplankton carbon by approximately one and two orders of magnitude, respectively. For example, Kepkay (2000) partitioned the carbon pools for the world ocean (in Gt C) as: DOC (200-700); POC (20); phytoplankton (1-11); and other biota (0.4). He further partitioned the DOC pool into a refractory low molecular weight component (120-630) and a bioavailable colloidal component (20-280). The combined DOC + POC is often referred to as “detritus” and represents a major source of carbon for the microbial food web.

In oceanic waters, the concentration of DOC generally decreases with depth from the surface to the level of the seasonal or permanent thermocline. In the MAB, Vlahos *et al.* (2002) and Del Vecchio and Blough (2004) found that DOC concentrations generally decreased from the coast to the shelf break.

Quantitative Approach for Estimates

Our estimation of the standing stocks of DOC is based on two steps. The first involves the construction of a generalized vertical profile of DOC, using the data from Guo *et al.* (1985) supplemented by near surface measurements of DOC made by Aluwihare *et al.* (1997) and by Vlahos *et al.* (2002). The second step involves the vertical integration of our generalized DOC profile from surface to bottom, using high resolution bathymetry data (1 km).

Guo *et al.* (1985) measured the vertical profile of DOC at a station in the MAB southeast of Chesapeake Bay during May 1993 (Figure 19.1). We have redrawn the data from Guo and Santschi in Figure 19.2 and show our estimates of DOC concentrations for sampling depths between 25 m and 2,500 m below the surface.

Aluwihare *et al.* (1997) measured DOC in surface waters of the MAB, on Georges Bank, and near shore waters near Woods Hole, MA (Figure 19.3). The mean DOC measured in these seven surface samples is 97.0 $\mu\text{M C}$.

Kepkay (2000) reported that DOC concentrations for the MAB ranged between 45 and 102 $\mu\text{M C}$. Vlahos *et al.* (2002) measured DOC in the MAB during surveys in April 1994, March 1996 and August 1996 (Figure 19.4) and reported that DOC concentrations ranged from 60 to 165 $\mu\text{M C}$ in surface waters and converged to 49 $\mu\text{M C}$ at depths below 200 m. The mean DOC in 137 samples from the upper 10 meters of the water column is 97.0 $\mu\text{M C}$, based on Table 3 in Vlahos *et al.* (2002). From these two studies, we assume a value of 97 $\mu\text{M C}$ represents a typical DOC concentration in surface water in our region. Our generalized vertical profile of DOC is illustrated in Figure 19.5.

The standing stocks of DOC were estimated for each region by combining the generalized DOC profile with a highly resolved map of bottom depth for the ecosystem (developed from the SRTM30 Plus bathymetry data set of Becker and Sandwell 2004). A frequency distribution of bottom depths was constructed for each region at a resolution of 1 meter and a spatial resolution of 1.25 x 1.25 km per pixel. (For the purpose of illustrating the bathymetric differences among the four regions, a less resolved frequency distribution is shown

in Figure 19.6.). For each bottom depth interval in increments of 1 meter, the generalized DOC profile was integrated from surface to bottom depth and these results were summed to yield the total and mean DOC concentration for each region (Table 19.1).

Results

Our estimate of average standing stocks of DOC in the MAB (44.5 g C m^{-2}) is in good agreement with the mean value 43.9 g C m^{-2} which we computed from the MAB shelf surveys reported by Vlahos *et al.* (2002; their Table 1).

Our estimates of particulate organic carbon (POC) standing stocks for the GOM (8.1 g C m^{-2}) assume an approximate 15:1 ratio between DOC and POC (Millero 1996; Kepkay 2000; Ogawa 2000). If we also apply a 5:1 ratio for POC:planktonic C ratio (Volkman and Tanoue 2002; Valiela 1995), then our estimated ratio of DOC:POC:Phytoplankton Carbon is 75:5:1, compared to the traditional oceanic water assumption of 100:10:1 (Parsons *et al.* 1984). The modern perspective on this ratio suggests that continental shelf waters are proportionally richer in POC and phytoplankton carbon than the oceanic water column, since coastal waters receive nutrient inputs from coastal land use which increases the rate of primary production and also receive inputs of POC from estuaries/bays. The planktonic carbon based on this simple proportionality scheme is 1.61 g C m^{-2} . This value is somewhat lower than our estimate of 2.01 g C m^{-2} for phytoplankton biomass derived from water column integrated chlorophyll concentrations (see in this document Section 2: Phytoplankton and Primary Production).

Given the operational separation of POC and DOC by filtration on glass fiber filters (nominal pore size $0.7 \mu\text{m}$), a portion of the POC is living, while there are small particles (viruses and some bacteria) in the “dissolved” DOC fraction. Some biological oceanographers analyze either ATP (adenosine triphosphate) or chlorophyll *a* and its degradation products (pheophytin or phaeophorbide) to estimate the living portion of POC. For example, off the California coast, the living fraction of POC varies from 14% to 79% in the upper 100 meters of the water column, decreasing to 6% at intermediate depths and below 3% at 500 to 1,000 meters below surface. Direct chemical composition of POC suggests that it is primarily carbohydrate and protein with small amounts of fat (Parsons *et al.* 1984). The water-soluble carbohydrate fraction disappears between 50 and 300 m, so that below 300-1000 m only the water-insoluble fraction persists. A variable fraction of the particulate detritus is calcium carbonate which can be mistaken for the non-living organic carbon component of POC (Parsons *et al.* 1984). The chemical and biological degradation of POC tends to decrease with depth (becomes more refractory). Bacteria and protozoa colonize some of these particles and their enzymatic activities convert POC to DOC. This colonization by microbes increases the nutritional value of POC for vertebrate/invertebrate detritivores.

In EMAX we assumed that 10% of the net primary production (P_{net}) was exported out of the mixed layer and transferred to the detritus compartment (noted as an assimilation efficiency of 90% in the EMAX spreadsheet). Cebrian (2002) utilized a value of 17% for the export of primary production out of the mixed layer. Net primary production is conventionally divided into recycled production (based on using ammonia) and new production (based on nitrate). In theory the new production in the euphotic zone is balanced by export production out of the mixed layer. The export ratio (ef) values range between 0.25 and 0.5 (Falkowski *et al.* 2003; Muller-Karger *et al.* 2005). A number of models have been developed to relate net production, temperature and/or depth to the ef value (Falkowski *et al.* 2003; Muller-Karger *et al.* 2005). We do not know how

much of the Pnet value estimated from ocean color satellite measurements is new versus recycled production, so we assumed that export was 15% of Pnet.

The DOC node was not explicitly incorporated as a food source for the microbial loop in the EMAX network given the uncertainty on its bioavailability to bacteria and microzooplankton (see discussion in those chapters). The POC node inputs include: phytoplankton dissolved production; phytoplankton that sediments out of the euphotic zone; and the detritus produced by egestion from each living node (since the assimilation efficiency is less than 100% of the consumption). The output from the POC node is consumed by bacteria, microzooplankton, mesozooplankton and various other larger benthic/pelagic filter feeders (see diet matrix in spread sheets). The microbial loop increases the efficiency of the grazing food chain by recycling the DOC excreted by phytoplankton and the POC egested from other nodes and linking it back to the grazing food chain through the use of POC as a food source. This recycled carbon passes through the indirect flow pathways in network models with the consequence that at the higher trophic levels (fish and marine mammals) much of the carbon received is via indirect pathways. This tendency is reflected in the recycling index parameter. The recycled carbon from the lower trophic levels allows the marine food web to be longer (more trophic levels) than that in lakes/estuaries. This is reflected to a degree in the average trophic level parameter for each node.

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Table 19.1. Average standing stocks of DOC for the MAB, SNE, GB and GOM ecoregions.

REGION	AREA (m ²)	DOC (g region ⁻¹)	Avg. DOC (g C m ⁻²)
MAB	5.73E+10	2.55E+12	44.5
SNE	6.46E+10	3.83E+12	59.2
GB	4.43E+10	3.29E+12	74.4
GOM	7.92E+10	9.66E+12	121.9



Figure 19.1. Location of station where Guo and Santschi (1997) measured the vertical profile of DOC.

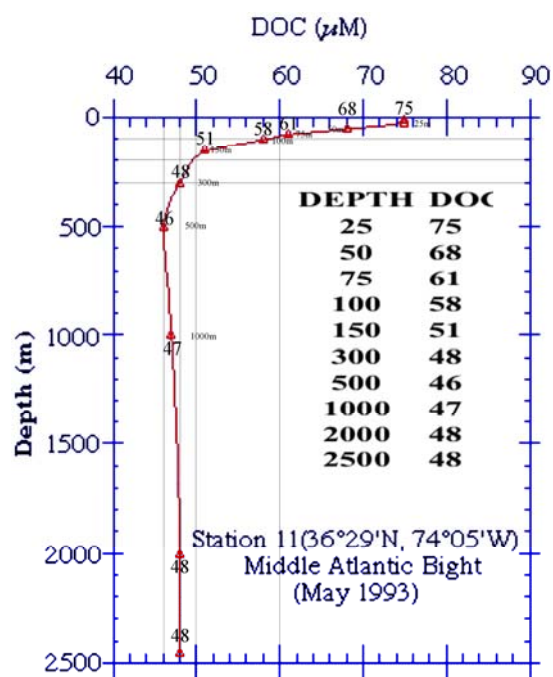


Figure 19.2. Vertical profile of DOC measured in the MAB, redrawn from Guo *et al.* (1995), showing our estimates of depth and DOC derived from the graph.

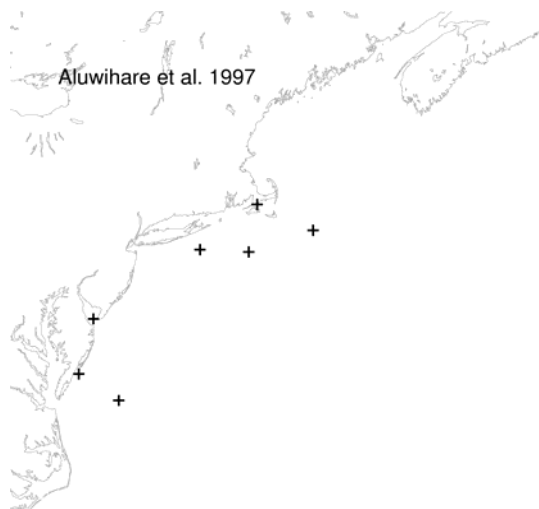


Figure 19.3. Sampling locations for DOC measurements made by Aluwihare *et al.* 1997.

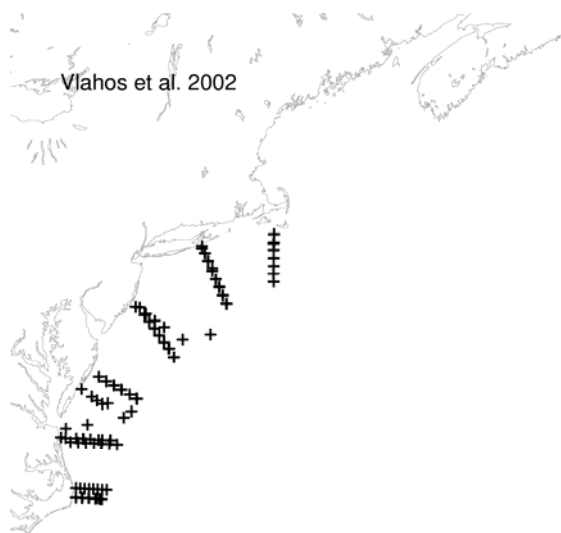


Figure 19.4. Sampling locations for DOC measurements made by Vlahos *et al.* 2002.

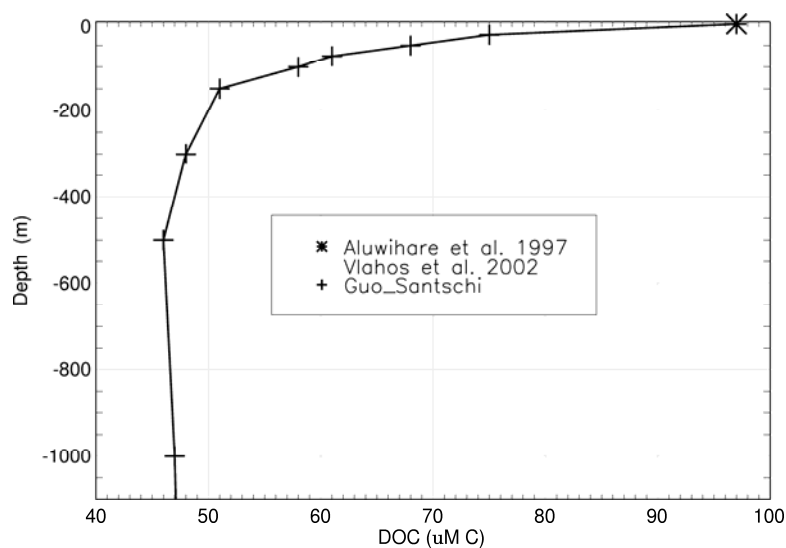


Figure 19.5. Generalized vertical profile of DOC concentration.

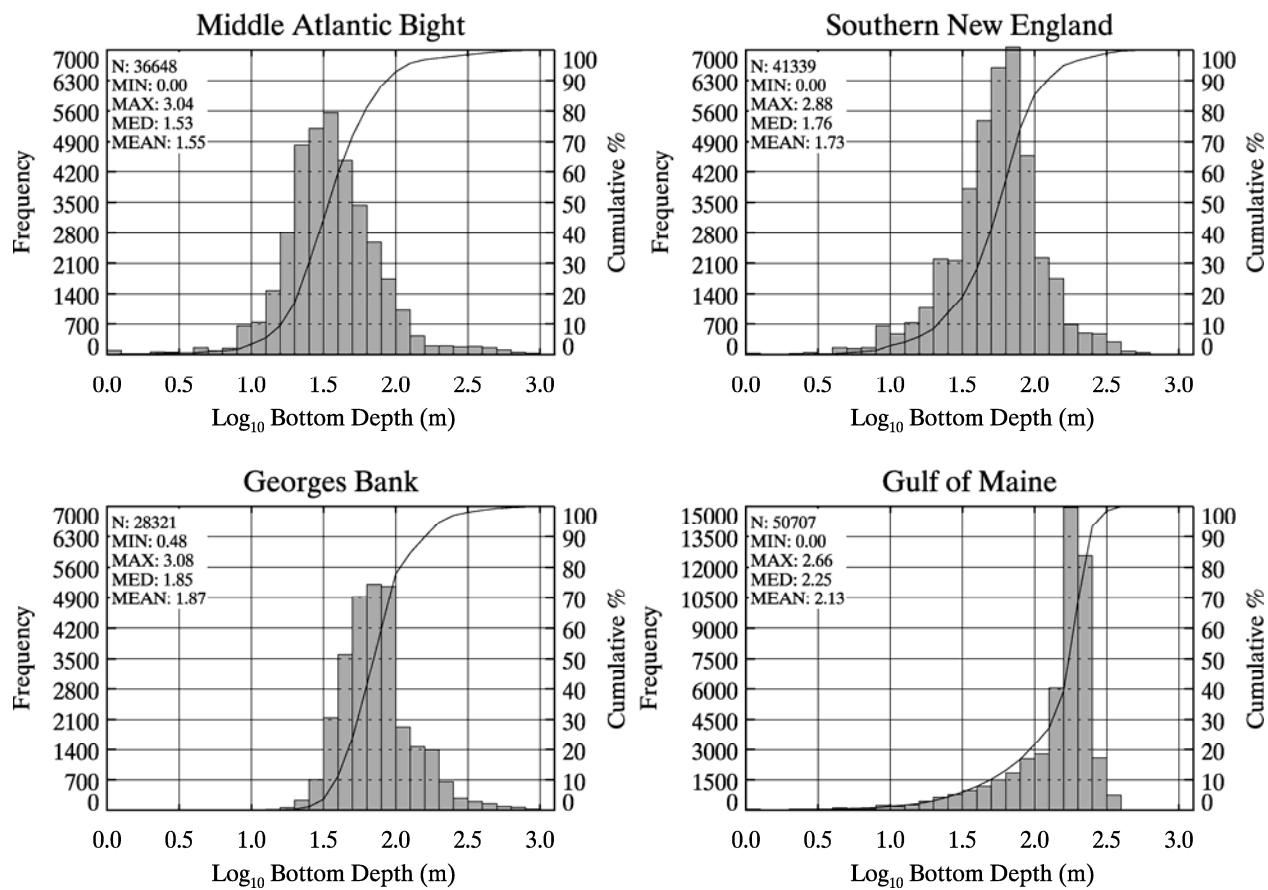


Figure 19.6. Frequency distribution of bottom depth for the GOM, GB, SNE, and MAB ecoregions based on data from a bathymetric map with 1.25 km resolution per pixel.

20. Fishery Removals (pelagic fisheries, demersal fisheries, discards)

Steven F. Edwards, Christopher M. Legault, Jon K.T. Brodziak, William J. Overholtz, and Laurel A. Col (nodes #32-34)

Landings

Commercial Landings

Data on U.S. and (where appropriate) Canadian landings (live weight in metric tons) of demersal and pelagic managed species from the years 1996-2000 were obtained from five general sources. Priority was given to sources that already compiled data into the ecoregion geographic classification. In some cases, various Stock Assessment Workshop (SAW) documents (<http://www.nefsc.noaa.gov/nefsc/saw>) and the related Groundfish Assessment Review Meeting (GARM) report (NEFSC 2002) provided data in the exact form necessary (e.g., Atlantic sea scallop from the 39th SAW and American plaice from the GARM report). In most cases, however, the available information was reported either for combinations of ecoregions (GARM [2002] and SAW documents) or for spatial units other than ecoregions (i.e., by Statistical Region or by State in the NMFS commercial database, including the small pelagic species, squids, and the remainder of the megabenthos). In either case, expert opinion from staff in the Population Dynamics Branch was used to allocate the values to the ecoregions. When only total regional landings were available, the expert opinion of one of the team members was relied on to allocate landings (bluefish, cusk, red hake, silver hake, white hake, offshore hake, river herring, black sea bass, American shad, striped bass, tilefish, Atlantic wolfish, and red crab). Landings for squid and the pelagic commercial group were obtained from NMFS data sources (CFDBS). These estimates were averaged over 1996-2000 and apportioned to the four areas by using area fished from the NMFS database. Commercial landings of large pelagic species were obtained from International Commission for the Conservation of Atlantic Tunas Standing Committee on Research and Statistics (ICCAT SCRS) reports. These data were apportioned by using distribution maps and making some assumptions about the percentage landed on the continental shelf.

Recreational Landings

Annual data (1996-2000) on the Type A (number of fish landed), Type B1 (number of fish discarded), and combined weight of both these categories were downloaded from the Marine Recreational Fisheries Statistics Survey (MRFSS) (<http://www.st.nmfs.gov/st1/recreational>) for the “all ocean combined” area of the Northeast Region (i.e., excluding bays and inland waters which lie outside the ecoregions). Given an assumption of equal size fish in both categories, Type A landings in weight (metric tons) were approximated by species. Species landings were allocated to the Gulf of Maine, Southern New England, and Mid-Atlantic Bight ecoregions in proportion to the length of each state’s contiguous shoreline. These results were aggregated by taxa.

Integrated Landings

Estimates of landings by the commercial and recreational fisheries were combined by ecoregion and averaged over 1996-2000 (Table 20.1).

Discards

Commercial Discards

Commercial discards for butterfish were obtained from the most recent stock assessment and included in the pelagic - commercial node (NEFSC 2004). No estimates of discards for herring and mackerel are available, but they are thought to be relatively small. Discard estimates for the large pelagic node were obtained from ICCAT SCRS documents. Discards for all the other groups were estimated as percentages of the landings, for example, discards for the demersal species were assumed to be 30% of landings during 1996-2000 (Alverson 1997). Discard estimates for megabenthos were assumed to be 0.0001 of biomass; gelatinous zooplankton, mesopelagics, and larval fish were assumed to be 0.000001 of biomass; and seabirds were 0.01 of biomass. Data for discards were summarized by group (node) and averaged over 1996-2000 (Table 20.2).

Recreational Discards

Total discards by the recreational fisheries is comprised of the Type B1 discard category mentioned above and mortality of Type B2 fish that are released alive (<http://www.st.nmfs.gov/st1/recreational>). Based on the same species-specific weights calculated above for Type B1 fish and the assumption of a 30% discard mortality for Type B2 fish, total discards were calculated by species for the recreational sector (metric tons). A fourth component of the MRFSS database is Type B2 fish that are released alive. Discards were allocated to ecoregion and aggregated by taxa as described above for landings.

Integrated Discards

Estimates of discards by the commercial and recreational fisheries were combined by ecoregion and averaged over 1996-2000 (Table 20.2).

References

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Table 20.1. Average annual landings (mt) for nodes used in the Ecopath-EcoNetwork analysis.

Node	Landings in mt			
	GOM	GB	SNE	MAB
Shrimp <i>et al.</i>	4924	0	0	0
Mesopelagics	0	0	0	0
Macrobenthos - polychaetes	0	0	0	0
Macrobenthos - crustaceans	0	0	0	0
Macrobenthos - molluscs	0	0	0	0
Macrobenthos - other	0	0	0	0
Megabenthos - filterers	7255	28287	106876	177728
Megabenthos - other	27320	1443	9788	860
Larval fish - all	0	0	0	0
Small Pelagics - commercial	69171	13056	28218	10770
Small Pelagics - other	1	0	1951	54770
Small Pelagics -anadromous	444	148	445	1377
Small Pelagics - squid	1095	1430	15865	12509
Medium Pelagics - (piscivores and other)	800	443	4137	3549
Demersals - benthivores	11274	11535	5336	1933
Demersals - omnivores	569	232	935	1680
Demersals - piscivores	23831	23206	18656	21297
Sharks - coastal	0	0	777	1460
Sharks - pelagics	19	35	74	62
Highly Migratory Species	144	149	487	607

Table 20.2. Average annual discards (mt) for nodes used in the Ecopath-Econetwork analysis.

Node	Discards in mt			
	GOM	GB	SNE	MAB
Gelatinous ZP	<1	<1	<1	<1
Shrimp <i>et al.</i>	1540	0	616	561
Mesopelagics	<1	<1	<1	<1
Macrobenthos- polychaetes	11	2	23	7
Macrobenthos- crustaceans	1	7	4	0
Macrobenthos- molluscs	15	5	28	0
Macrobenthos- other	57	36	25	0
Megabenthos- filterers	2387	8486	33280	54192
Megabenthos- other	8199	433	3358	524
Larval fish- all	<1	<1	<1	0
Small Pelagics- commercial	10369	1306	10556	2919
Small Pelagics - other	12	0	1808	5556
Small Pelagics -anadromous	44	15	45	138
Small Pelagics- squid	1322	143	2540	1347
Medium Pelagics (piscivores and other)	240	133	1241	1106
Demersals- benthivores	3401	3460	1625	734
Demersals- omnivores	180	70	643	1100
Demersals- piscivores	7149	6962	5597	6389
Sharks-coastal	0	0	233	438
Sharks-pelagics	6	10	22	19
Highly Migratory Species	43	45	146	182
Sea Birds	5	6	4	

21. Other Removals

Debra L. Palka (node #29)

Background

Ship strikes remove baleen whales from the ecosystem, and bycatch or entanglements in fishing gear remove pinnipeds, baleen whales, and odontocetes. This section describes how the biomass of these removals was calculated.

Data Sources and Quantitative Approach for Biomass of Removal Estimates

The average annual numbers of animals removed by ship strikes and fishing gear are documented in Waring *et al.* (2004). These numbers were decomposed into the numbers by species within each of the EMAX ecoregions (Table 21.1). The biomass (in metric tons) of the removals of species k in ecoregion i was then estimated as the product of the number of removals of species k in ecoregion i and the average weight of an individual (in kg). The total biomass (in metric tons) of removal within ecoregion i is the sum of biomass removed over all species k :

$$(EQ. 21.1) \quad \text{biomass of removals}_i = \sum_{\text{species } k} (\text{number of individuals removed}_{ki} \bullet \text{average weight}_k) / 1000.$$

Biomass removed per area (in g m^{-2}) was calculated as biomass removed by ship strikes and fishing gear (in metric tons) per area of the ecoregion (in km^2 ; Table 21.1).

Example Results

Baleen whales were removed by both fishing gear and ship strikes. The most biomass per area (in g m^{-2}) removed by fishing gear was from Southern New England and Georges Bank, and the most removed by ship strikes was from the Mid-Atlantic Bight and Southern New England ecoregions (Table 21.1; Figure 21.1). The amount of odontocetes biomass removed due to fishing gear was fairly evenly distributed among the four ecoregions, where most of the biomass was from harbor porpoises, common dolphins and white-sided dolphins (Figure 21.2A). Nearly all the pinniped biomass removed by fishing gear was from harbor seals in the Gulf of Maine region (Figure 21.2B).

References

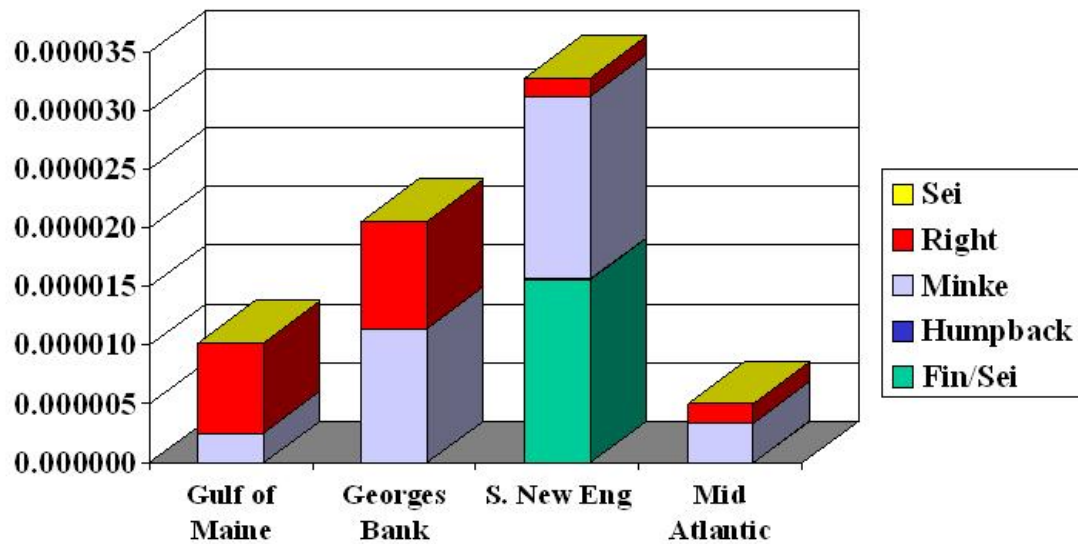
Waring, G; Pace, RM; Quintal, JM; Fairfield, CP; Maze-Foley, K, eds. 2004. U.S. Atlantic and Gulf of Mexico marine mammal stock assessments – 2003. *NOAA Technical Memorandum NMFS-NE-182*. www.nefsc.noaa.gov/nefsc/publications/tm/tm182

Table 21.1. By species and ecoregion, average number of animals removed per year by ship strikes and fishing gear.
Note: blank cell indicates no animals were removed.

Species	Average Number of Animals Removed Per Year								Total
	By Ship Strikes				By Fishing Gear				
	GOM	GB	SNE	MAB	GOM	GB	SNE	MAB	
Fin W.	0.2		0.4	0.8			1		2.4
Hump W.	0.1		0.1	0.2					0.4
Minke W.	0.2				0.2	0.5	1	0.2	2.1
Right W.		0.2	0.2	0.2	0.6	0.4	0.1	0.1	1.8
Sei W.			0.2						0.2
Beaked									0
Bottlen D.							26	134	160
Common					29	17	22	76	144
Grampus						3			3
Har. Por.					160	77	40	33	310
Kogia									0
Pilot W.						11	51	16	78
Sperm W.						0.2			0.2
Spotted D.									0
Striped D.									0
Whiteside					40	21	25		86
Grey S.					131				131
Harbor S.					953		2		953
Harp S.					106			3	106
Hooded S.					16				16
TOTAL	0.5	0.2	0.9	1.2	1435.8	130.1	168.1	262.3	1994.1

Figure 21.1. Biomass (in g m^{-2}) of removals of baleen whales (A) by fishing gear and (B) by ship strikes.

A. By fishing gear.



B. By ship strikes.

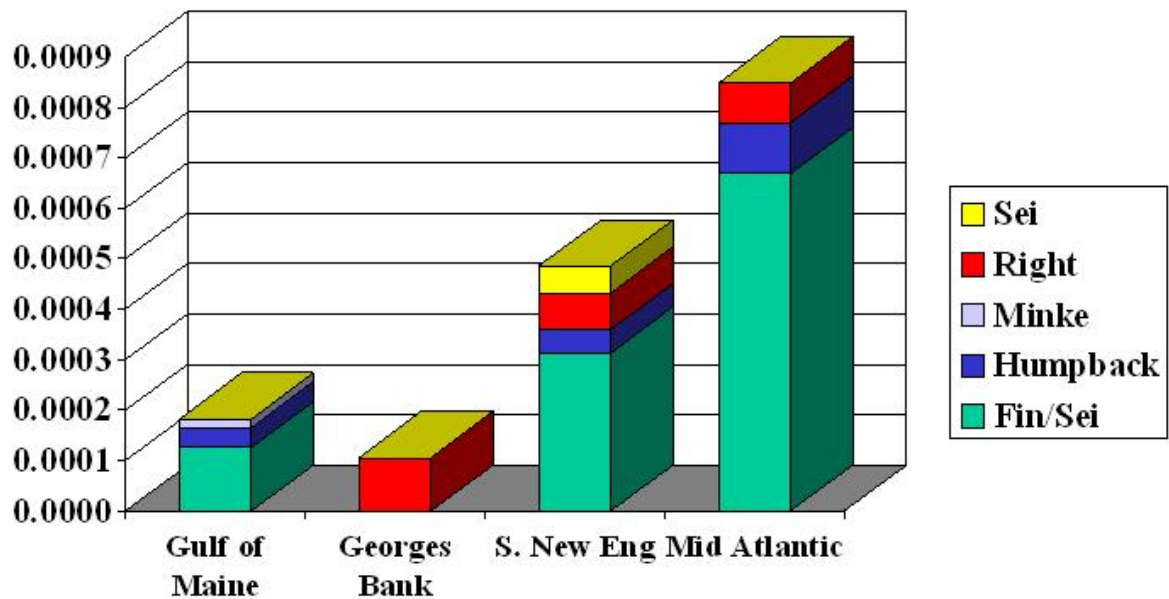
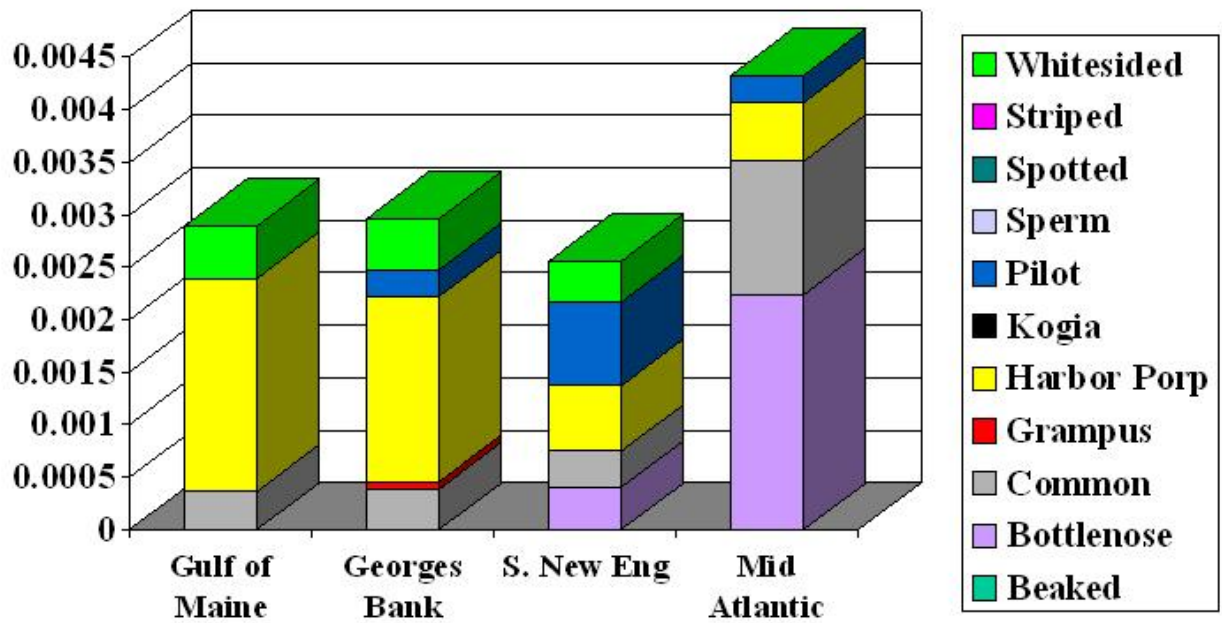
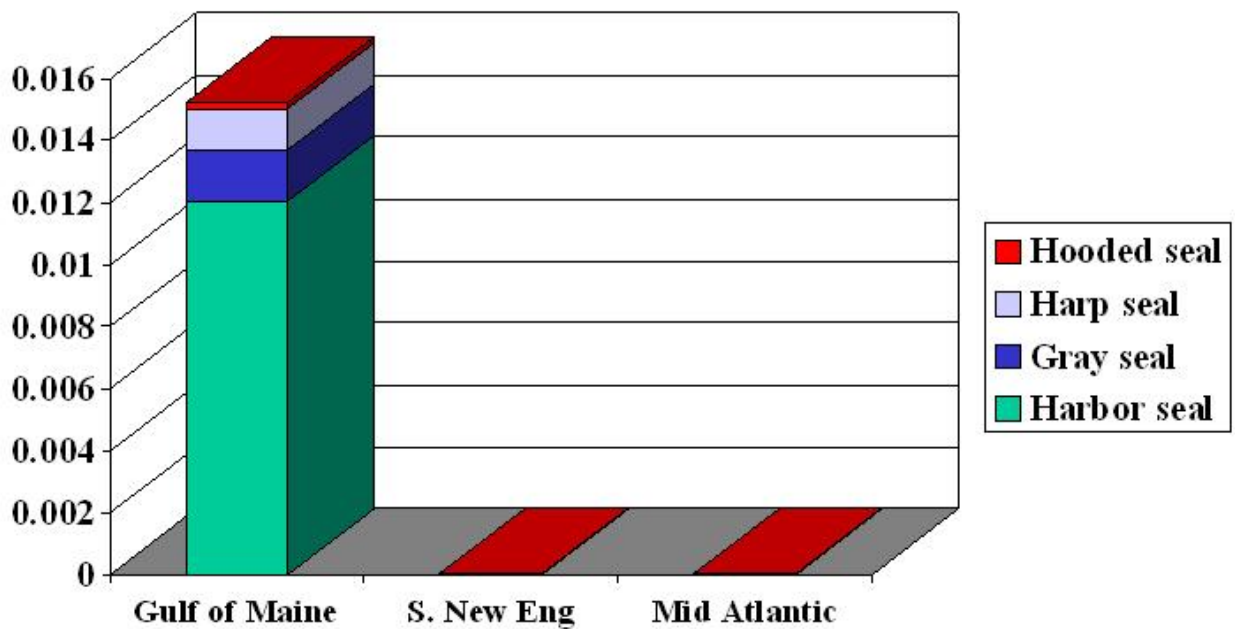


Figure 21.2. Biomass of removals by fishing gear of (A) odontocetes and (B) pinnipeds.

A. Odontocetes.



B. Pinnipeds.



22. Consumption and Diet Composition Matrix

Jason S. Link

Interaction Matrix - Fish

The standard Northeast Fisheries Science Center (NEFSC) bottom trawl survey program has been executed annually since 1963 (Grosslein 1969; Azarovitz 1981; NEFC 1988). During these surveys, food habits data are collected from a variety of species. These multi-species surveys were designed to monitor trends in abundance and distribution and to provide samples to study the ecology of the large number of fish and invertebrate species inhabiting the region. The surveys have generally utilized a 36' Yankee otter trawl towed at approximately 3.5 knots for 30 minutes at each station. Trawl stations were selected using a stratified random design. Within each stratum, stations were assigned randomly, and the number of stations allotted to a stratum was in proportion to its area. Station allotments were approximately one station per 200 square nautical miles. The surveys were conducted at depths of 27 m to 366 m; however, greater depths were occasionally sampled in the deep canyons along the continental shelf break. Once onboard, predators were sorted to species, weighed to the nearest 0.1 kg and measured to the nearest cm. Sex and maturity were determined, and subsamples of key species were eviscerated for feeding ecology studies.

The NEFSC has collected fish food habits data for over 30 years. Starting in 1973, individual stomach samples for selected species were preserved at sea in 10% buffered formalin for later prey identification. Individual stomach preservation was continued until 1981 for an expanding list of species. Prey weight (to 0.01 g), number, percent composition, total stomach weight (to 0.01 g), and lengths of fish prey (mm) were determined upon examination in the laboratory. Prey identification was to the lowest taxon feasible. In 1981 the stomachs of major species such as Atlantic cod, haddock, silver hake, yellowtail flounder, winter flounder, Atlantic herring, and Atlantic mackerel continued to be individually preserved, but prey of all other species were examined and identified at sea. In addition, a conversion from mass (g) to volumetric measurement of prey (to 0.1 cm³) was initiated. Data on prey composition (%), numbers, and lengths were also collected shipboard. Since 1985, all stomach samples have been processed and prey identified at sea. To account for potential differences in the resolution of prey taxonomy between in-lab and at-sea sampling, we grouped most prey, particularly invertebrates, into broad prey categories (i.e., Class or Order). The exception was fish prey, which were maintained at the lowest feasible level. A conversion factor of 1.1 was used to convert prey volumes to weights based upon regression analyses (Link and Almeida 2000) similar to other studies (Bowman, unpublished manuscript; Tanasichuk *et al.* 1991; Garrison and Link 2000). For further details of the food habits data, see Link and Almeida (2000).

We estimated mean stomach contents (to 0.01 g) and diet composition (as a percentage of weight) for each EMAX predator node category by EMAX prey node category.

Interaction Matrix - Other Nodes

For those nodes for which we did not have direct diet information, we assumed that the values for each EMAX predator's diet composition fell within the range described for similar species in the literature. These percentages were adapted based on a suite of criteria (including

suitability and known feeding patterns from local species of similar biology) so that each predator's diet summed to 100%. Examples of values can be found in the subject literature for each node or in food web compilations (e.g., Kenny *et al.* 1985, Overholtz *et al.* 1991, Pauly *et al.* 1995, Hammill *et al.* 1997, Kenny *et al.* 1997, Sigurjonsson and Vikingsson 1997, Stenson *et al.* 1997, Barros and Clarke 2002, Link 2002.). Values for the EMAX interaction matrix are in Table 22.1. We also show the connections for each node in Figure 22.1.

Fish Consumption

We calculated the percent composition by weight of each major EMAX prey category in relation to the total amount consumed by each EMAX fish predator. Using a two-stage cluster method we weighted these values by the number of tows and the number of fish in a tow (see equations below). Link and Almeida (2000) provide a more thorough discussion of the statistics behind these methods and their calculation.

Based on an evacuation rate model (Eggers 1977; Elliot and Persson 1978), daily consumption estimates (C_d) were calculated for an average predator in each of the EMAX fish groups as

$$(EQ. 22.1) \quad C_{d_i} = 24 \cdot E_i \cdot \bar{S}_i^\gamma,$$

where 24 is the number of hours in a day, i is the species of fish, γ is a constant (usually assumed to be equal to 1). The evacuation rate E is

$$(EQ. 22.2) \quad E_i = \alpha e^{\beta T_p},$$

where α and β are both fitted constants and T is temperature. Based on literature values and sensitivity analyses, we set α and β to 0.004 and 0.115, respectively (Durbin *et al.* 1983; Overholtz *et al.* 1999). We used a mean temperature for two (approximately semiannual) time periods (p) per year: 1) winter and spring surveys combined, and 2) summer and fall surveys combined (D. Mountain and M. Taylor; NEFSC, Woods Hole, Massachusetts, unpublished data).

From Equation 22.1 above, \bar{S}_i is the mean total stomach contents (g), such that

$$(EQ. 22.3) \quad \bar{S}_i = \frac{\sum_{t=1}^{n_t} n_{it} \cdot \bar{S}_{it}}{n_t},$$

where n_t is the number of tows for all strata sampled, n_{it} is the number of predator stomachs within a tow, and

$$(EQ. 22.4) \quad \bar{S}_{it} = \frac{\sum_{k=1}^{n_{it}} S_{itk}}{n_{it}}$$

is the mean stomach weight of predator i in tow t , where k represents an individual fish.

The daily consumption rates from both semiannual time periods were combined into a total, annual population level consumption rate (C):

$$(EQ. 22.5) \quad C_i = \sum_1^p (C_{d_i} \cdot d_p),$$

where d is the number of days in each time period p (182.5 for each, corresponding to the bottom trawl survey; NEFSC 1998).

The total amount of a particular EMAX prey (j) consumed by an EMAX fish predator (i), (C_{ij}), was estimated by multiplying the total consumption (Equation 5) by the (fixed) percentage (D_{ij}) of each prey comprising the diets of these predators, such that

$$(EQ. 22.6) \quad C_{ij} = C_i \cdot D_{ij},$$

where D_{ij} is

$$(EQ. 22.7) \quad D_{ij} = \frac{\bar{S}_{ij}}{\bar{S}_i},$$

and where \bar{S}_i is from equation 3 and \bar{S}_{ij} is

$$(EQ. 22.8) \quad \bar{S}_{ij} = \frac{\sum_{i=1}^{n_i} n_{it} \cdot \bar{S}_{ijt}}{n_i},$$

where

$$(EQ. 22.9) \quad \bar{S}_{ijt} = \frac{\sum_{k=1}^{n_{it}} S_{ijk}}{n_{it}}.$$

Given the short time span of the project, we chose to use a fixed diet composition for the EMAX prey (D_{ij}). All other parameters were estimated for two periods each year and the annual consumption was allocated according to the fixed diet proportion, D_{ij} . We examined the mean, minimum, and maximum consumption estimates to ascertain the range of possible EMAX prey removals by these fish predators.

It was determined that we needed a per capita consumption rate for each EMAX fish predator. Thus, the factor in Equation 22.5 was adopted and integrated across a year to give an annual average without scaling to population abundance.

The average sizes (weight) of the EMAX fish predators were then calculated to give an estimate of per capita biomass, B_i . The annual estimate of consumption, C_i , was then used with the estimate of average biomass, B_i , to calculate the C:B ratio.

These estimates were calculated for the following nodes:

- Small Pelagics - commercial
- Small Pelagics - other
- Small Pelagics - squid

Small Pelagics - anadromous
Medium Pelagics - (piscivores and other)
Demersals - benthivores
Demersals - omnivores
Demersals – piscivores

For examples of where this approach has been previously used see Link *et al.* (2002), Link and Garrison (2002), and Overholtz *et al.* (1999, 2000).

For all other EMAX nodes, literature values of C:B were used to estimate consumption. Further details are given in sections in this volume specific to each group.

Integrating Consumptive Removals

For each EMAX node, the total consumption was multiplied by the diet composition vector (Equation 22.6) to allocate the amount removed via consumption by each predator node for all EMAX prey nodes. These vectors were then summed across the cross-vector (or row) for each prey item to calculate a total amount of biomass removed per year for each EMAX node.

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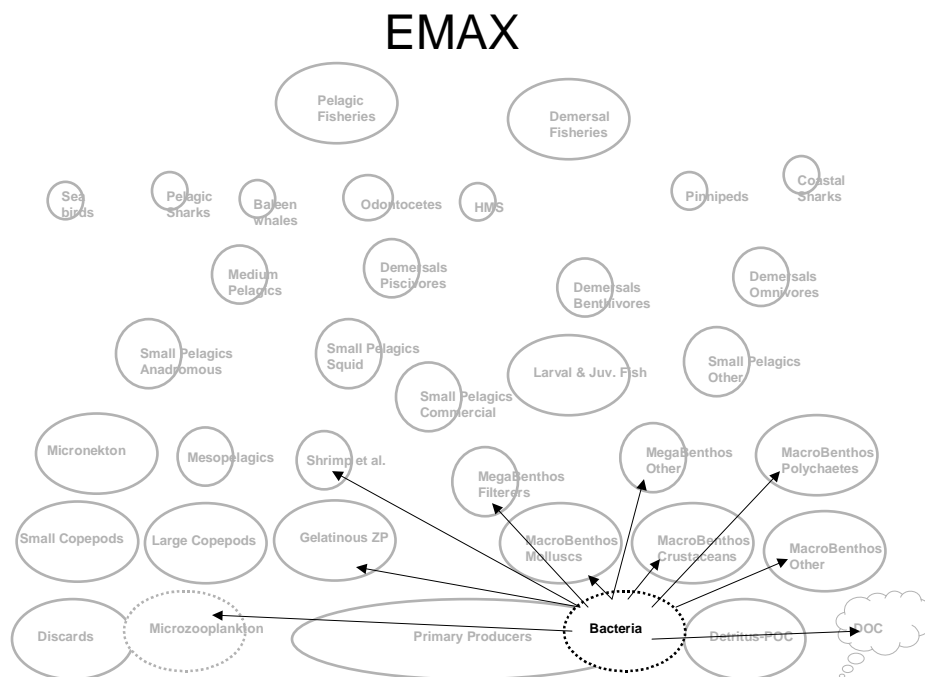
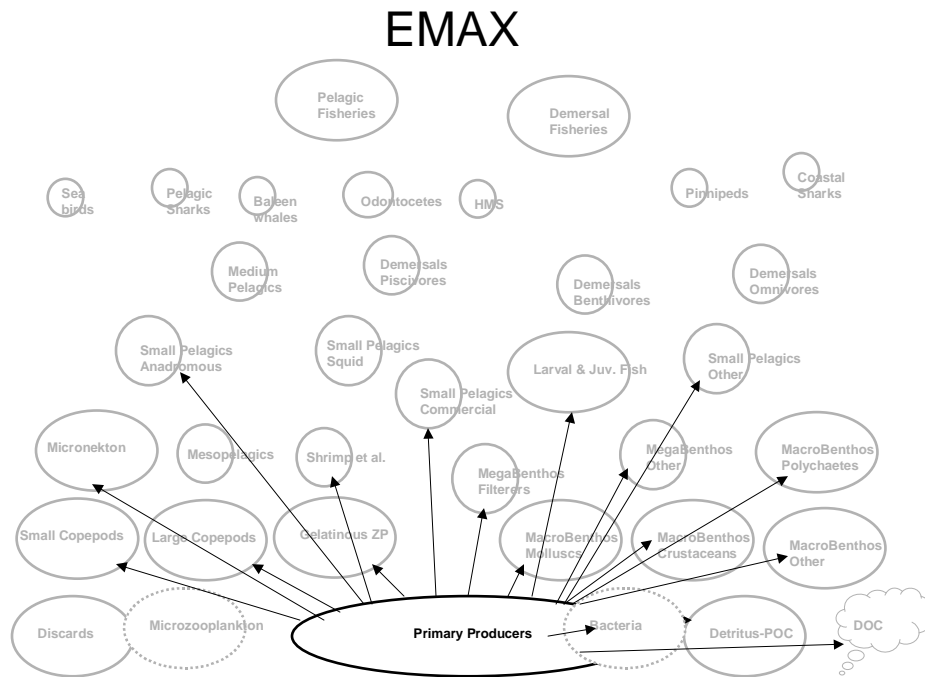
Table 22.1. Example EMAX interaction matrix for GOM. Flows are from row to column.

	Phytoplankton - Primary Producers	Bacteria	Microzooplankton	Small Copepods	Large Copepods	Gelatinous Zooplankton	Micronekton	Macrobenthos - polychaetes	Macrobenthos - crustaceans	Macrobenthos - molluscs	Macrobenthos - other	Megabenthos - filterers	Megabenthos - other	Shrimp <i>et al.</i>
Phytoplankton - Primary Producers	0	15	15	61	46	8.6	11.4	10.8	12.0	37.9	14.9	60	0	5.4
Bacteria	0	0	40	0	0	2	0	26.0	10.6	17.5	16.0	20	12	32
Microzooplankton	0	0	10	20	5	5	0	0	0	0	0	0	0	0
Small Copepods	0	0	0	8	28	33	51.3	0	1.1	0	0	0	0	0
Large Copepods	0	0	0	0	10.3	36	22.9	0	2.1	0	0	0	0	0
Gelatinous Zooplankton	0	0	0	0	5	2.1	0	0	0	0	0	0	0	0
Micronekton	0	0	0	0	0	0	2.9	0	0	0	0	0	0	10.8
Macrobenthos - polychaetes	0	0	0	0	0	0	0	9.4	10.0	0	5.0	0	6.7	0
Macrobenthos - crustaceans	0	0	0	0	0.3	0	0	1.7	10.4	0	5.0	0	6.7	5.4
Macrobenthos - molluscs	0	0	0	0	0	0	0	0.9	14.2	6.7	14.9	0	20.1	0
Macrobenthos - other	0	0	0	0	0.4	0	0	5.1	10.4	5.2	8.0	0	20.1	7.5
Megabenthos - filterers	0	0	0	0	0	0	0	0.3	1.1	1.1	0.4	0	3.3	0
Megabenthos - other	0	0	0	0	0	0	0	0.33	1.0	1.1	5.0	0	14.3	0
Shrimp <i>et al.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1.5
Larval and Juvenile Fish - all	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Small Pelagics - commercial	0	0	0	0	0	1.5	0	0	0	0	0	0	0	0
Small Pelagics - other	0	0	0	0	0	0.4	0	0	0	0	0	0	0	0
Small Pelagics - squid	0	0	0	0	0	0.3	0	0	0	0	0	0	0	0
Small Pelagics - anadromous	0	0	0	0	0	0.1	0	0	0	0	0	0	0	0
Medium Pelagics - piscivores & other	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Demersals - benthivores	0	0	0	0	0	0	0	0	0.4	0	0.5	0	0.7	0
Demersals - omnivores	0	0	0	0	0	0	0	0	0.2	0	0.3	0	0.4	0
Demersals - piscivores	0	0	0	0	0	0	0	0	0	0	0.3	0	0.4	0
Sharks - coastal	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Highly Migratory Species	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pinnipeds	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Baleen Whales	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Odontocetes	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sea Birds	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Discards	0	0	0	0	0	0	0	0.5	0.5	0.5	0.7	0	3.3	5.4
Detritus - POC	0	85	35	11	5	10	11.5	45	26	30	29	20	12	32

Table 21.1, continued.

	Small Pelagics - commercial	Small Pelagics - other	Small Pelagics - squid	Small Pelagics - anadromous	Medium Pelagics - piscivores & other	Demersals - benthivores	Demersals - omnivores	Demersals - piscivores	Sharks - pelagics	Highly Migratory Species	Pinnipeds	Baleen Whales	Odontocetes	Sea Birds
Phytoplankton - Primary Producers	1.1	15.7	0	1.1	0	0	0	0	0	0	0	0	0	0
Bacteria	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Microzooplankton	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Small Copepods	11.7	11.5	0	7.9	0	0	0	0	0	0	0	5.8	0	0
Large Copepods	42.6	64.1	9	87.4	0	0	0	0	3	0	0	46.2	0	3
Gelatinous Zooplankton	2.1	3.1	0	0	0.1	0.5	1.2	0.1	0	7.2	0	0.1	0.3	0
Micronekton	21.3	4.2	45	1.9	0	6.1	3.5	2.2	0	0	7.4	28.9	2.5	12.3
Macrobenthos - polychaetes	1.1	0	0	0.3	0	14.6	17.7	1.1	0	0	0	0	0	0
Macrobenthos - crustaceans	6.7	0.2	13.5	0.6	1.2	18.1	17.7	1.1	1	0	0	5.8	0	0
Macrobenthos - molluscs	1.1	0.2	0	0	0	12.2	17.7	3.3	0	0	0	1.2	0	0
Macrobenthos - other	1.1	0.3	1.5	0	1.2	18.0	11.8	10.9	1	0	0	2.3	0	0
Megabenthos - filterers	0	0	0	0	0	5.2	4.3	1.1	0	0	0	0	0	0
Megabenthos - other	0	0	0	0	19	9.5	11.8	2.2	0	0	0	0.7	0	0
Shrimp <i>et al.</i>	0	0	6.8	0	2.4	2.1	0.4	15.3	0	0	0	0	0	6.2
Larval and Juvenile Fish - all	10.6	0.7	15	0.8	1.2	0	1.2	1.1	0	0	0	0	0	0
Small Pelagics - commercial	0	0	1.4	0	35.5	6	5.8	27	21	14.4	44.5	5.8	35.2	27.3
Small Pelagics - other	0	0	1.5	0	3.6	0.2	0.2	5.6	5	72.1	14.8	0.6	19	23.5
Small Pelagics - squid	0	0	6.1	0	3.6	0.4	0.2	5.5	16	6.3	0	1.1	25.4	6.1
Small Pelagics - anadromous	0	0	0.2	0	2.4	0	0	0.2	2	0	11	0.3	4.6	4
Medium Pelagics - piscivores & other	0	0	0	0	0.1	0	0	0	13	0	0.1	0	0.1	0.1
Demersals - benthivores	0.2	0	0	0	11.9	3.7	1.3	1.1	5	0	7.4	0	0	0
Demersals - omnivores	0.2	0	0	0	5.9	0.6	1	0.4	8	0	7.4	0	6.3	3.7
Demersals - piscivores	0.2	0	0	0	11.9	0.4	0.6	21.8	7	0	7.4	0	6.3	2.5
Sharks - coastal	0	0	0	0	0	0	0	0	3	0	0	0	0	0
Highly Migratory Species	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Pinnipeds	0	0	0	0	0	0	0	0	3	0	0	0	0	0
Baleen Whales	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Odontocetes	0	0	0	0	0	0	0	0	2	0	0	0	0.3	0
Sea Birds	0	0	0	0	0	0	0	0	3	0	0	0	0	0
Discards	0	0	0	0	0	1.2	2.4	0		0	0	0	0	11.3
Detritus - POC	0	0	0	0	0	1.2	1.2	0	5	0	0	1.2	0	0

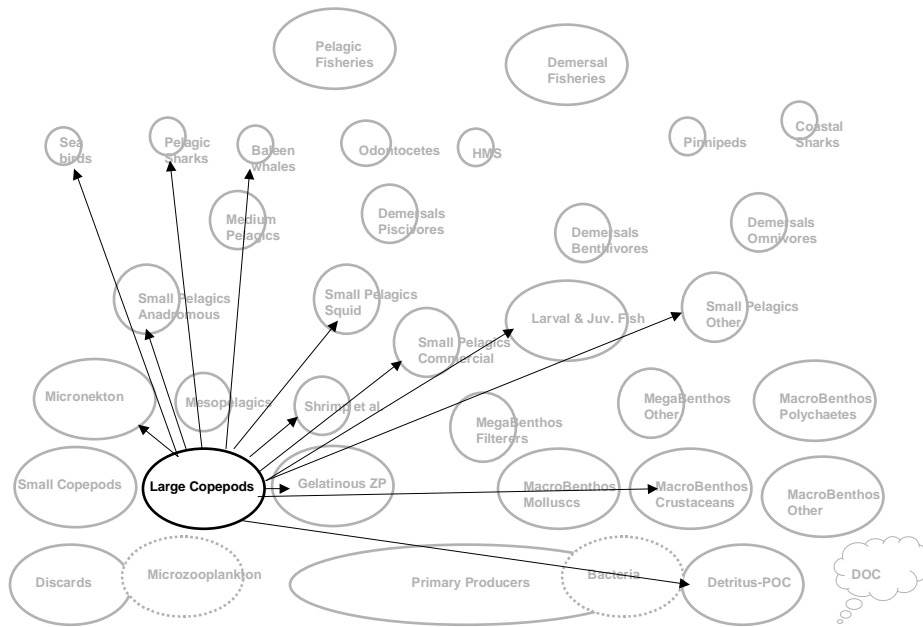
Figure 22.1. Network connections for each node, showing the flows from one node to its consumer nodes.



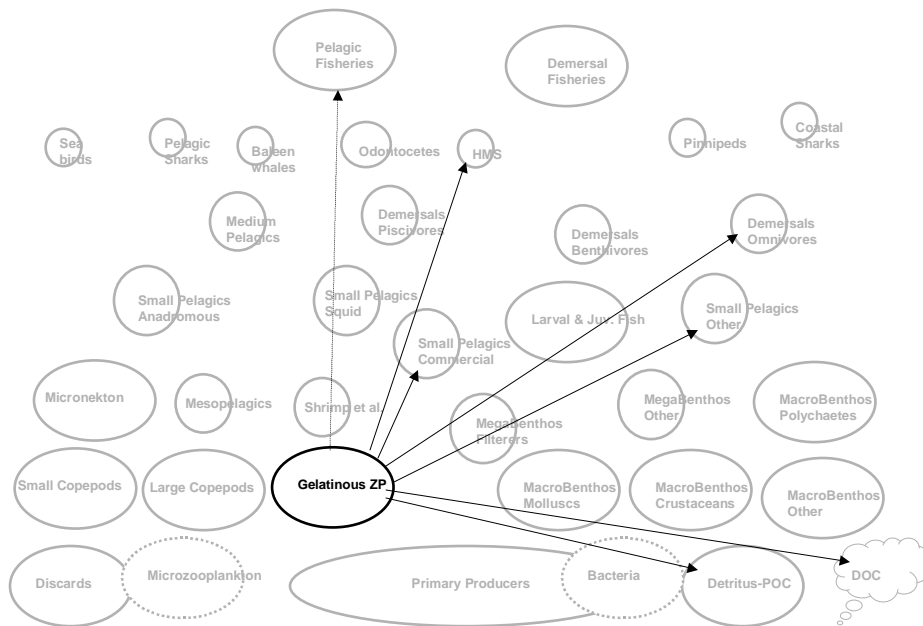
The diagram illustrates the marine food web with energy flow indicated by arrows. At the base are **Primary Producers** (green oval) and **Bacteria** (dotted oval). **Primary Producers** flow energy to **Microzooplankton** (dotted oval), **Discards** (green oval), **Small Copepods** (green oval), **Large Copepods** (green oval), **Gelatinous ZP** (green oval), **Detritus-POC** (green oval), and **DOC** (cloud). **Bacteria** flow energy to **Microzooplankton** and **Detritus-POC**. **Microzooplankton** flows energy to **Discards**, **Small Copepods**, **Large Copepods**, and **Gelatinous ZP**. **Discards** flows energy to **Small Copepods**, **Large Copepods**, and **Gelatinous ZP**. **Small Copepods** flows energy to **Large Copepods** and **Gelatinous ZP**. **Large Copepods** flows energy to **Gelatinous ZP**. **Gelatinous ZP** flows energy to **MicroBenthos** (green oval). **MicroBenthos** flows energy to **MacroBenthos Molluscs** (green oval), **MacroBenthos Crustaceans** (green oval), and **MacroBenthos Other** (green oval). **MacroBenthos Molluscs** flows energy to **MacroBenthos Crustaceans** and **MacroBenthos Other**. **MacroBenthos Crustaceans** flows energy to **MacroBenthos Other**. **MacroBenthos Other** flows energy to **Demersal Omnivores** (green oval). **Detritus-POC** flows energy to **DOC**. **DOC** flows energy to **Primary Producers**. The diagram also shows various other trophic levels: **Sea birds**, **Pelagic Sharks**, **Baleen whales**, **Odontocetes**, **HMS**, **Pinnipeds**, **Coastal Sharks**, **Medium Pelagics**, **Small Pelagics Anadromous**, **Small Pelagics Squid**, **Small Pelagics Commercial**, **Larval & Juv. Fish**, **Small Other Pelagics**, **Micronekton**, **Mesopelagics**, **Shrimp et al.**, **MegaBenthos Filters**, **MegaBenthos Other**, **MacroBenthos Polychaetes**, **Demersal Piscivores**, **Demersal Benthivores**, **Demersal Omnivores**, **Pelagic Fisheries**, and **Demersal Fisheries**.

The diagram illustrates the flow of energy and matter from **Small Copepods** to various higher trophic levels. **Small Copepods** are the central node, with arrows pointing to **Micronekton**, **Mesopelagics**, **Small Pelagics Commercial**, **Larval & Juv. Fish**, **Gelatinous ZP**, **MacroBenthos Molluscs**, and **Detritus-POC**. From these nodes, further arrows lead to higher trophic levels: **Micronekton** to **Small Pelagics Endemic** and **Small Pelagics Squid**; **Mesopelagics** to **Small Pelagics Commercial** and **Small Pelagics Endemic**; **Small Pelagics Commercial** to **Larval & Juv. Fish** and **Small Pelagics Endemic**; **Larval & Juv. Fish** to **Small Pelagics Endemic** and **Small Pelagics Commercial**; **Gelatinous ZP** to **Small Pelagics Commercial** and **Small Pelagics Endemic**; **MacroBenthos Molluscs** to **MacroBenthos Crustaceans** and **MacroBenthos Other**; **Detritus-POC** to **DOC**. The diagram also shows other trophic levels like **Pelagic Fisheries**, **Demersal Fisheries**, **Sea birds**, **Pelagic Sharks**, **Baleen whales**, **Odontocetes**, **HMS**, **Pinnipeds**, **Coastal Sharks**, **Demersals Piscivores**, **Demersals Benthivores**, **Demersals Omnivores**, **Microzooplankton**, **Discards**, **Primary Producers**, **Bacteria**, and **DOC**.

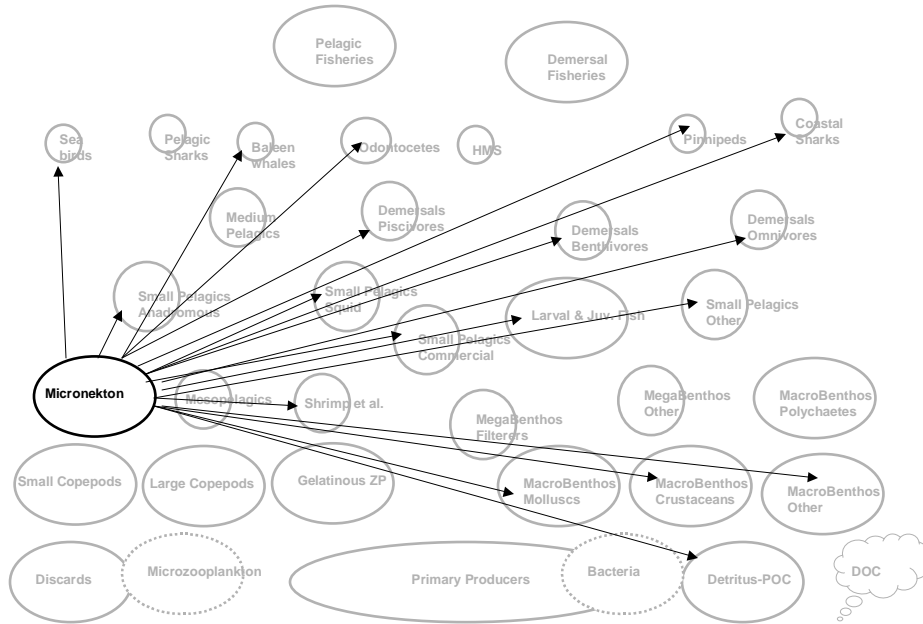
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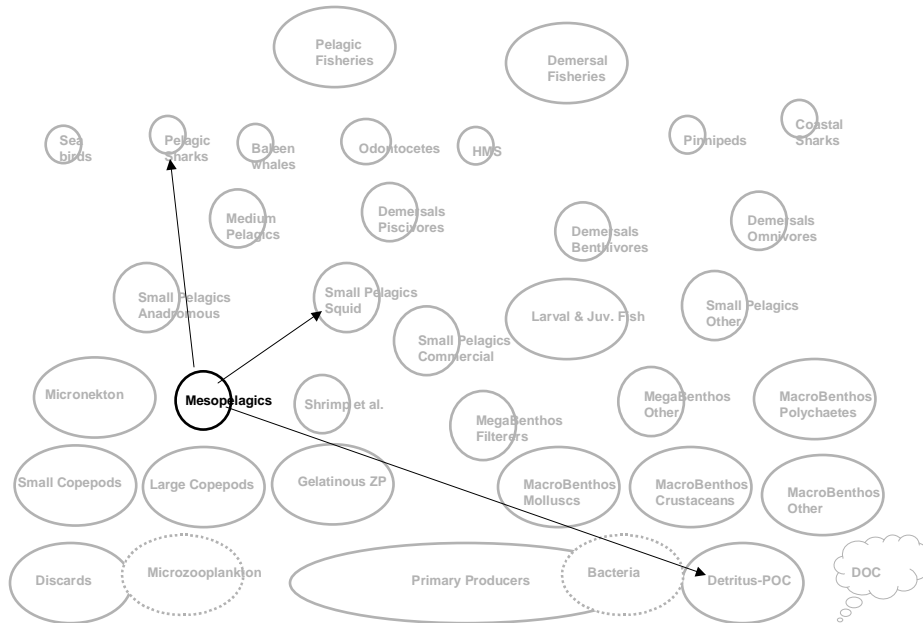
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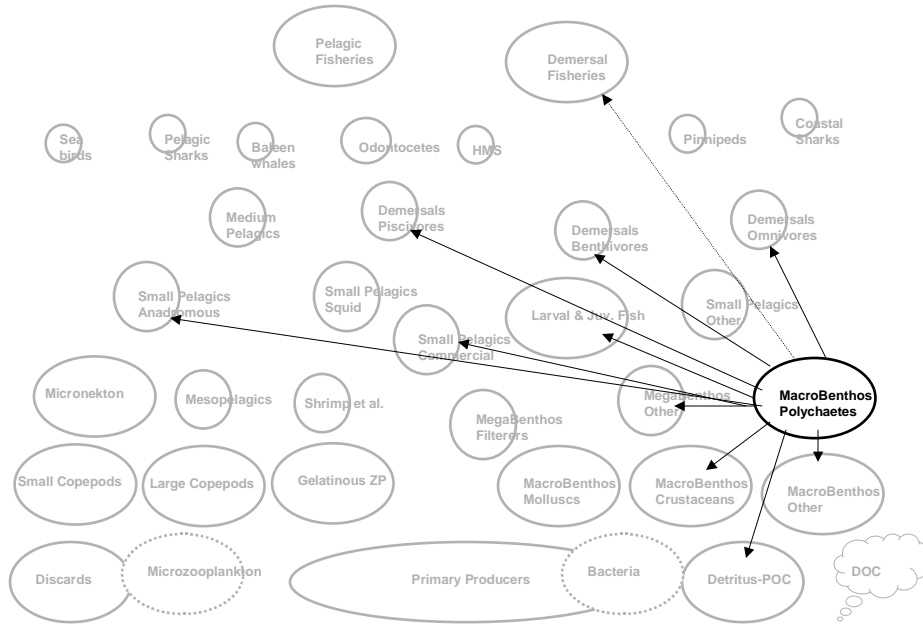
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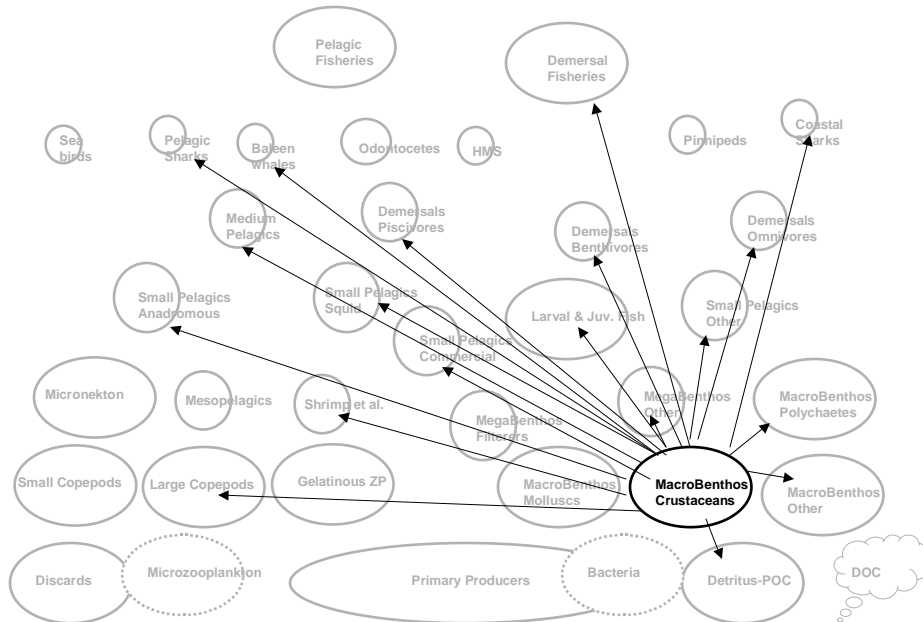
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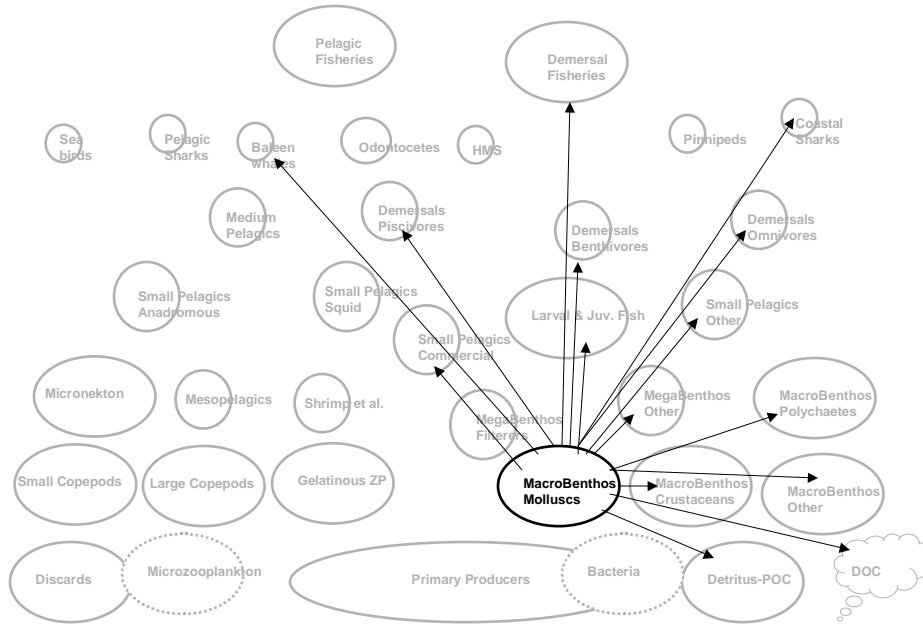
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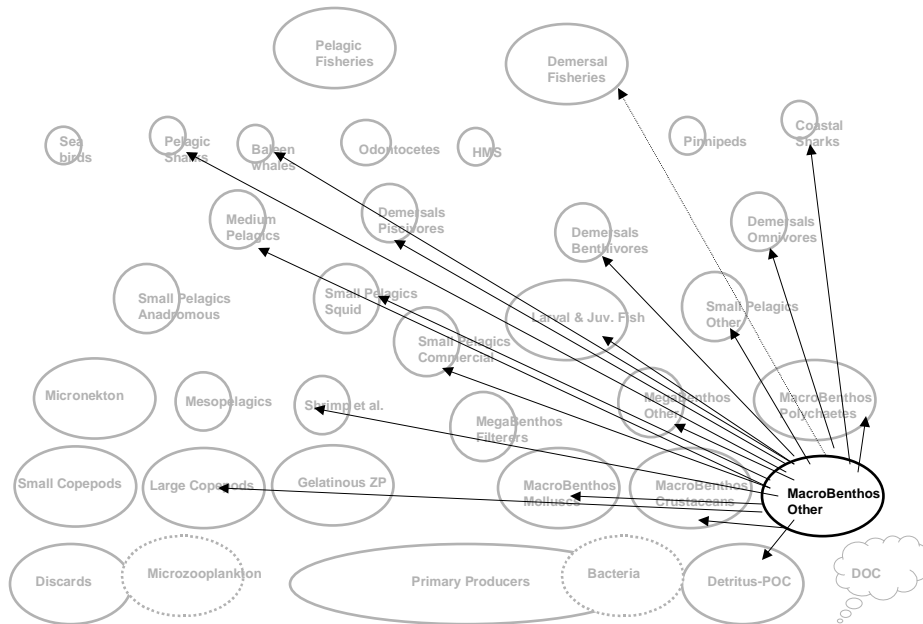
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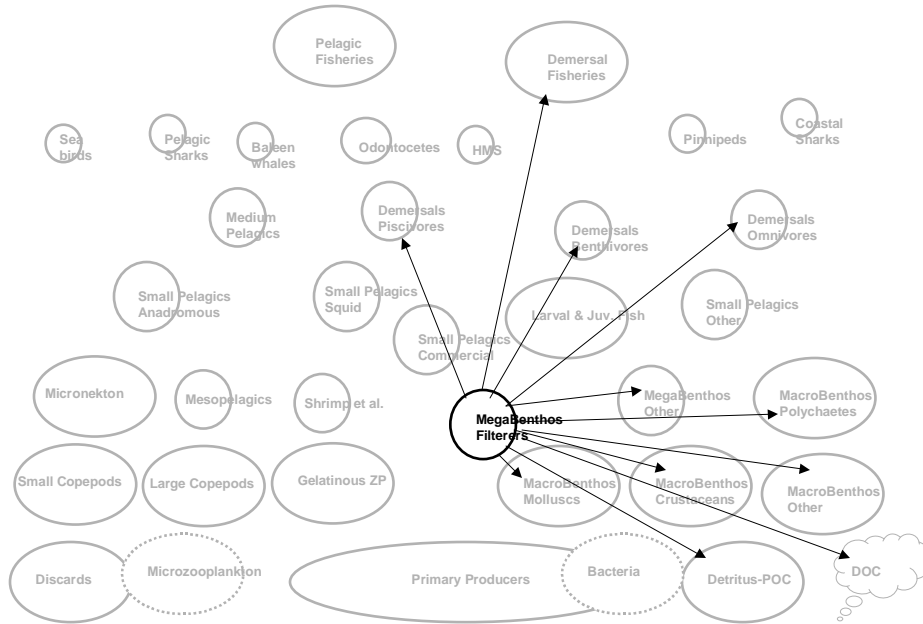
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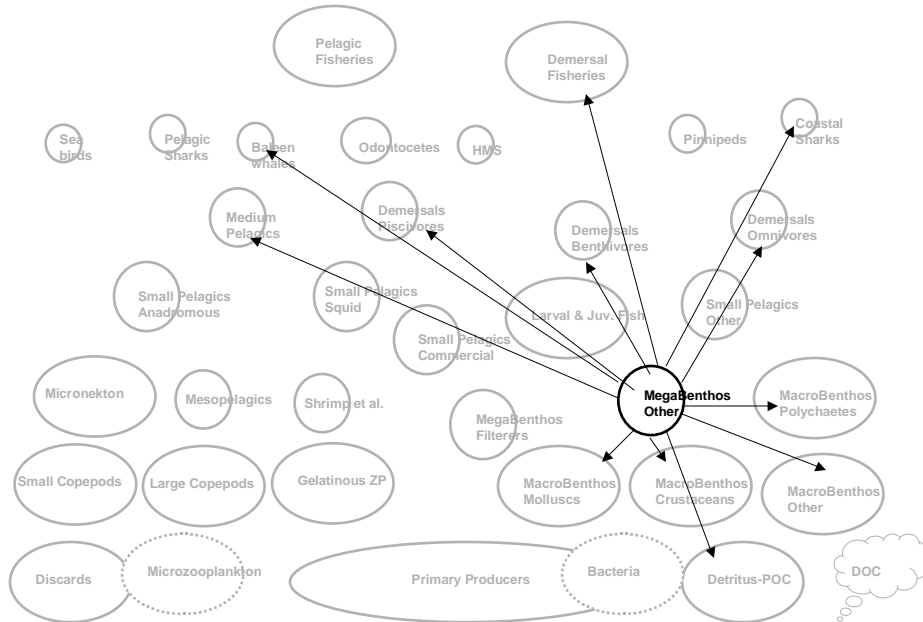
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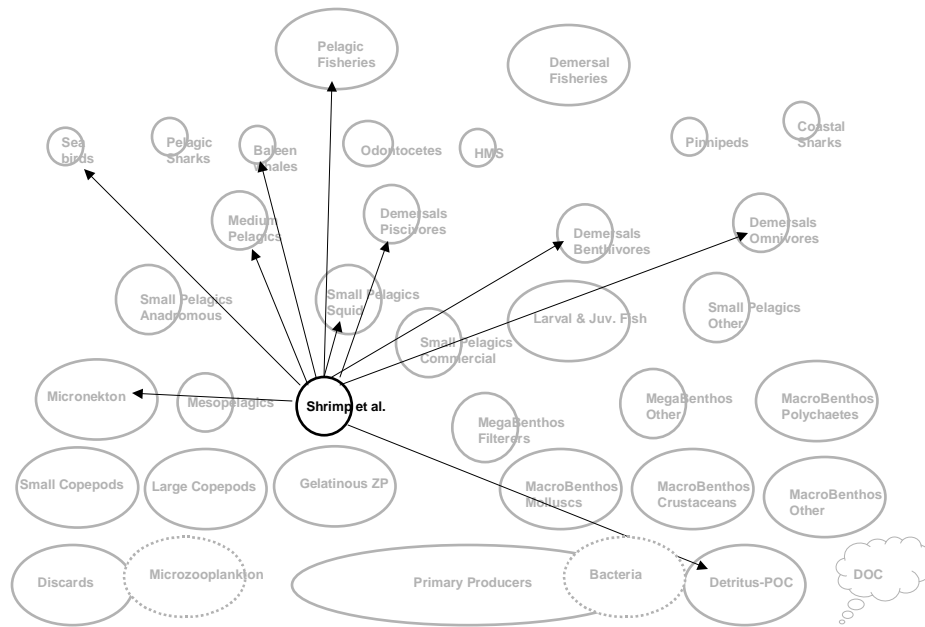
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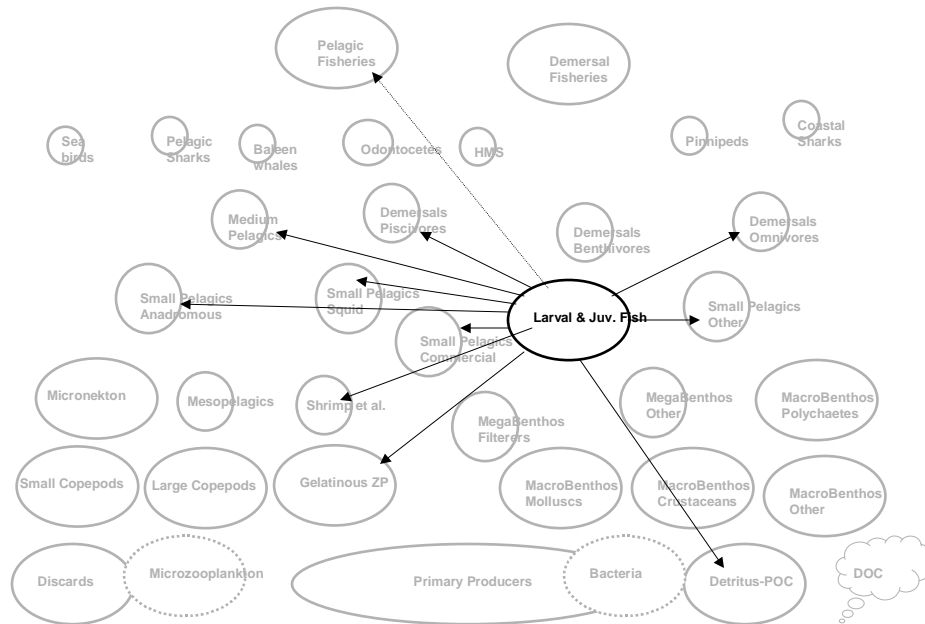
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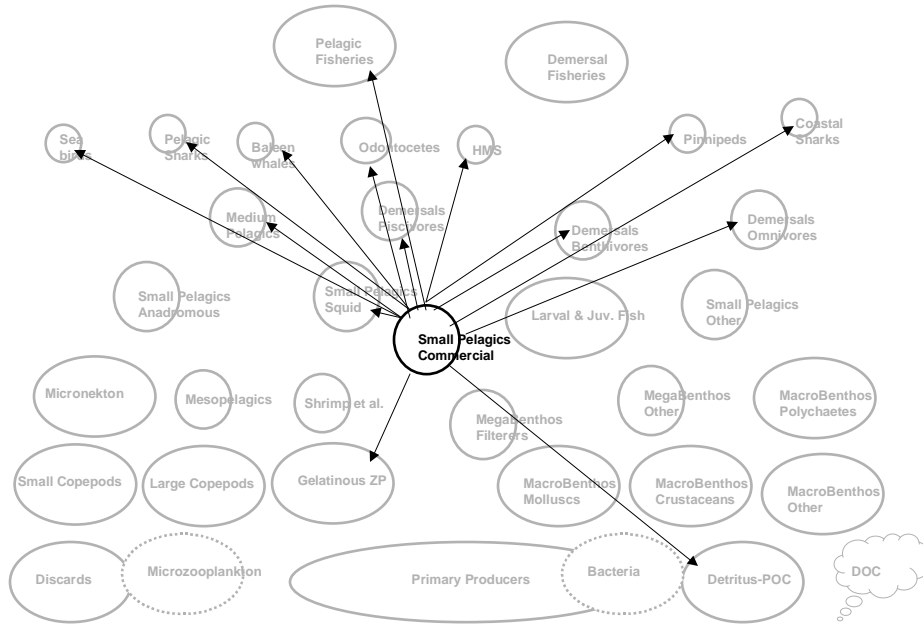
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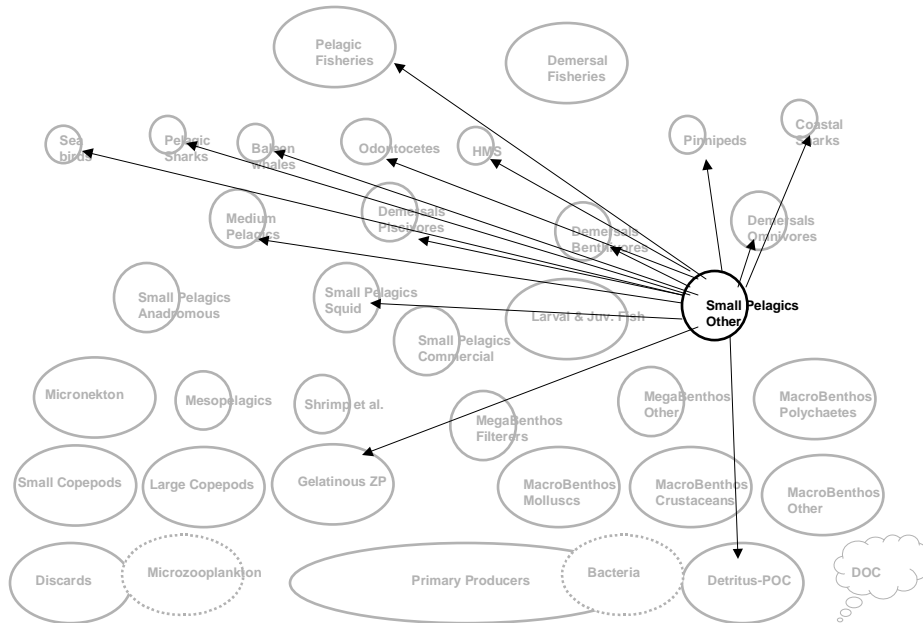
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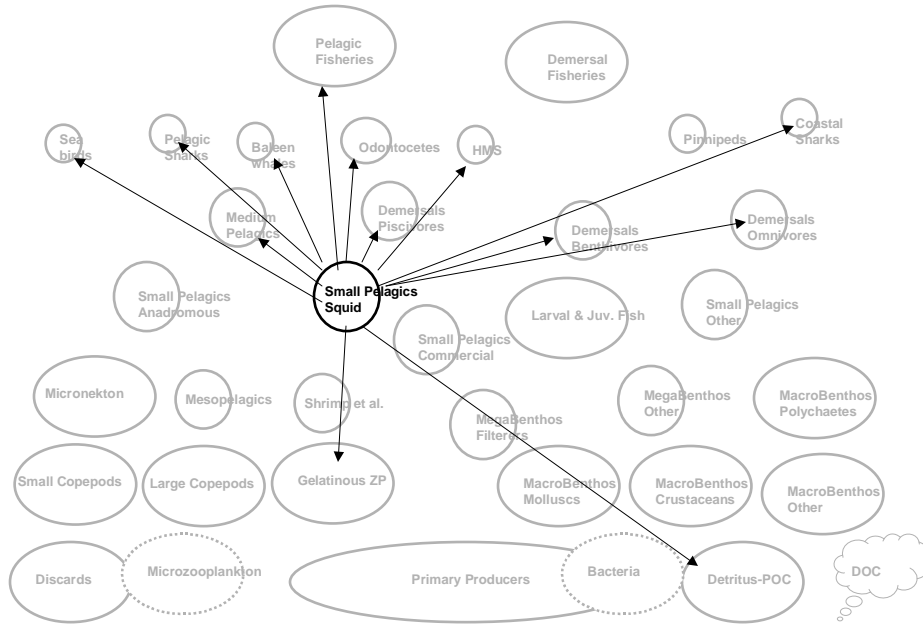
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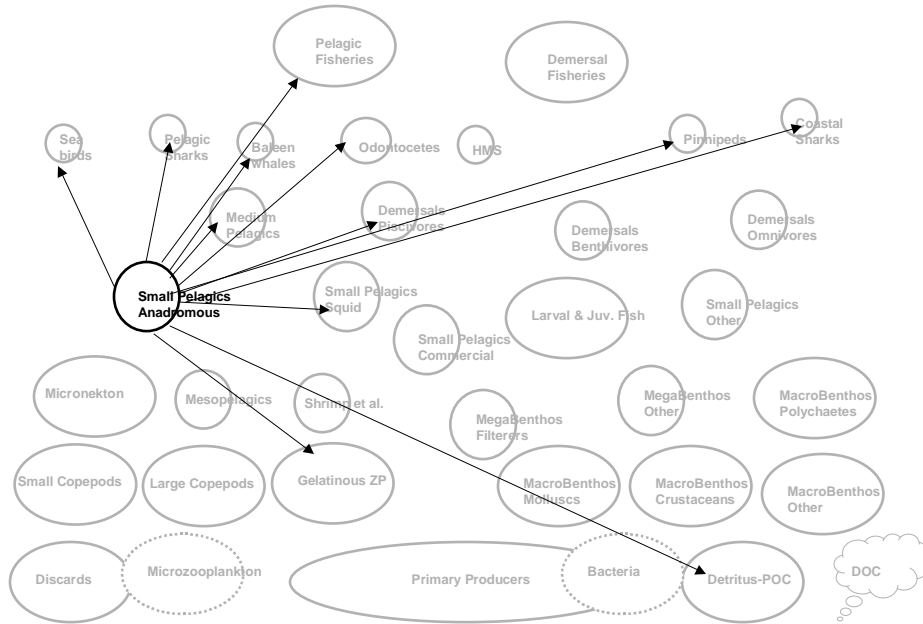
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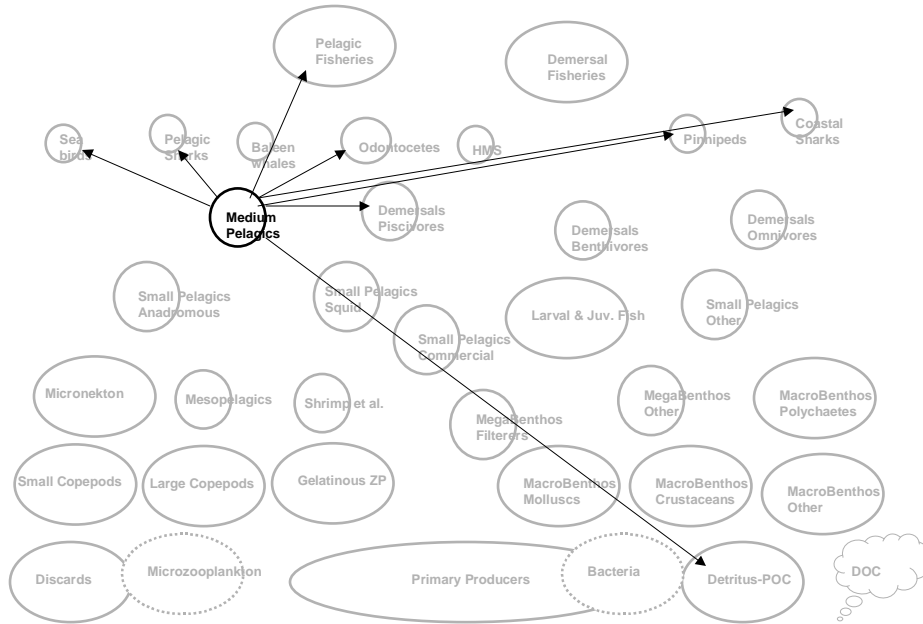
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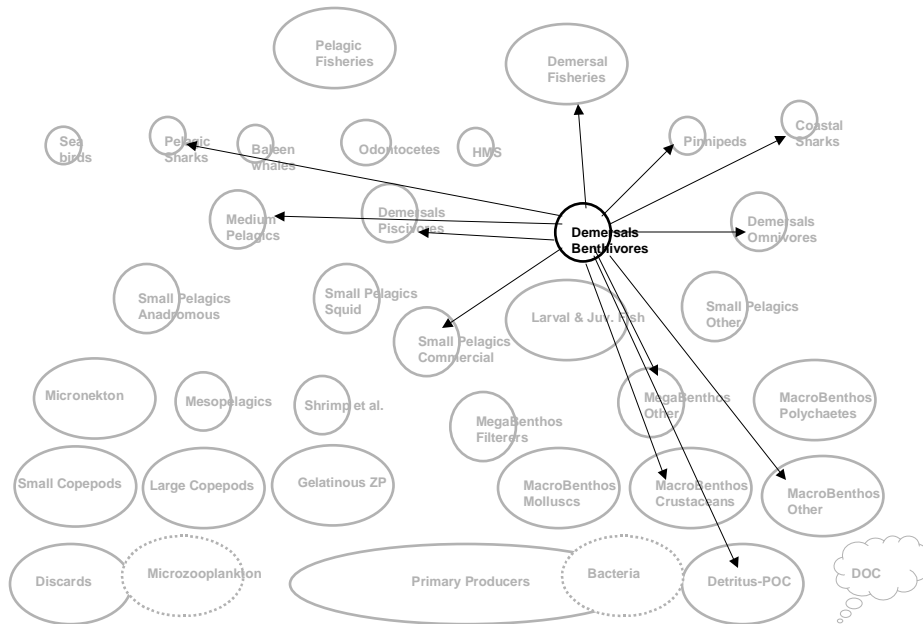
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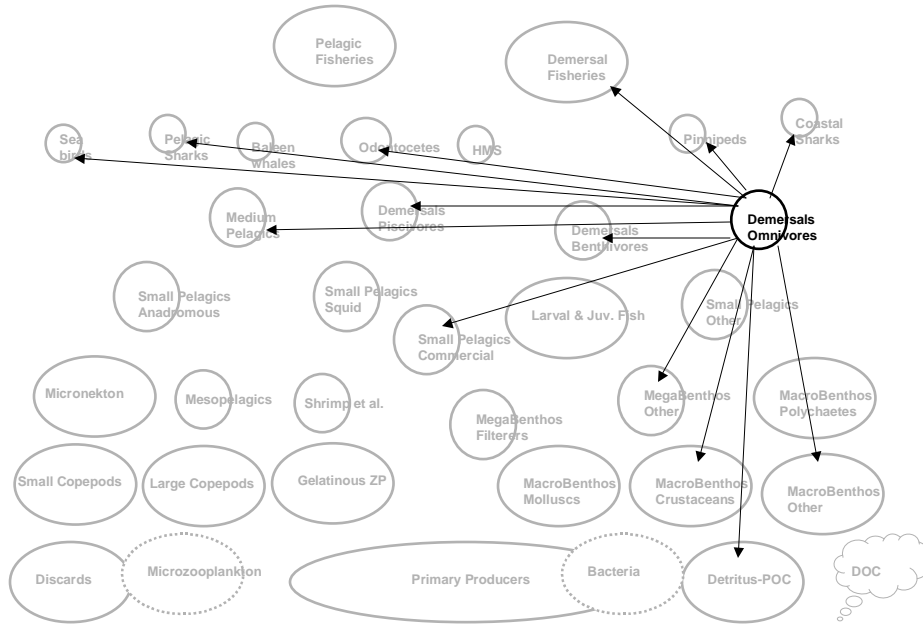
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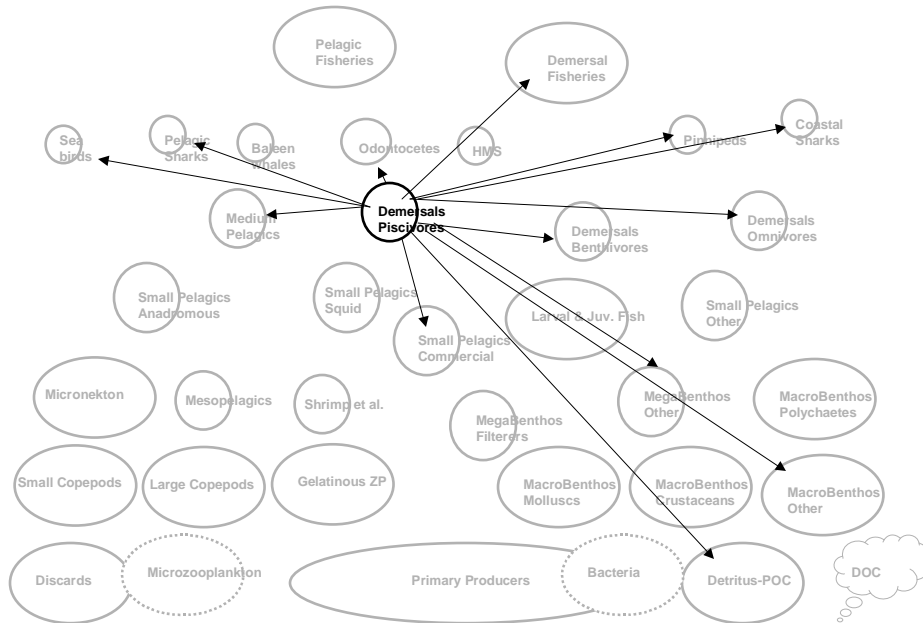
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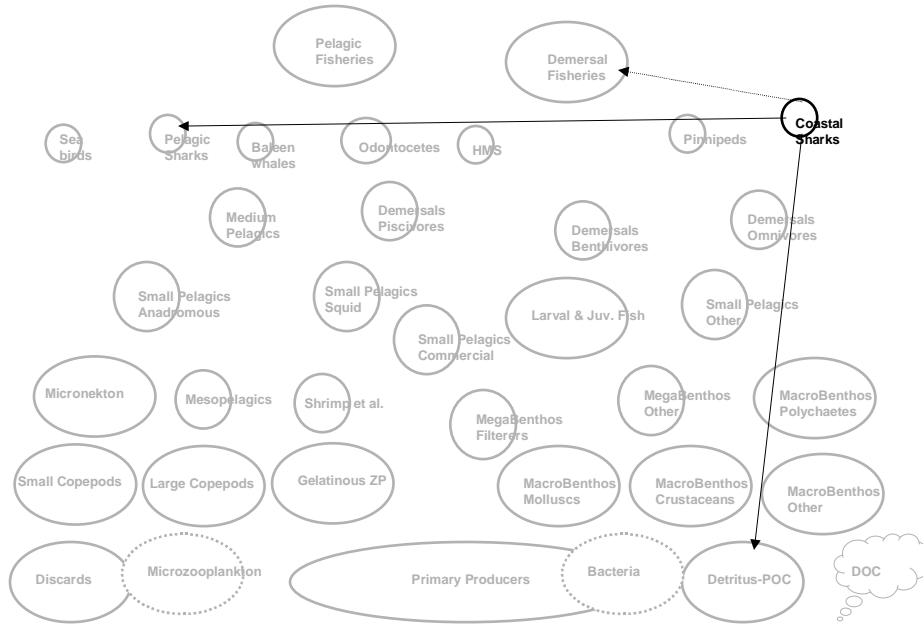
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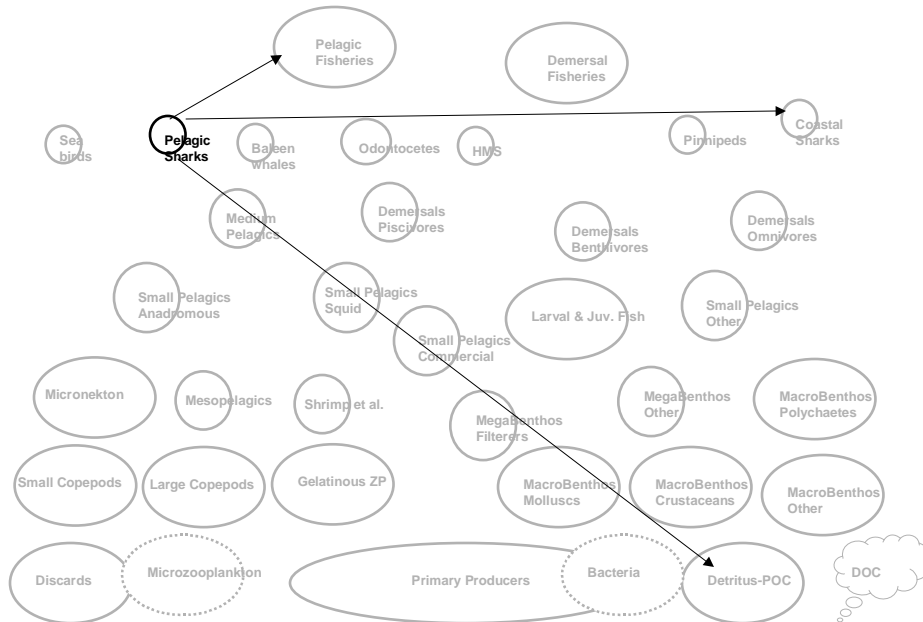
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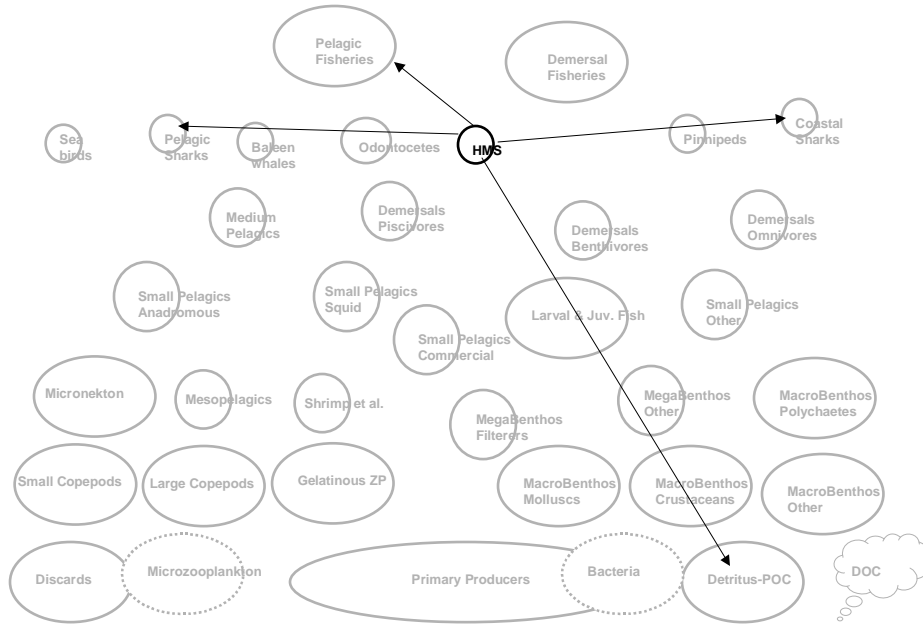
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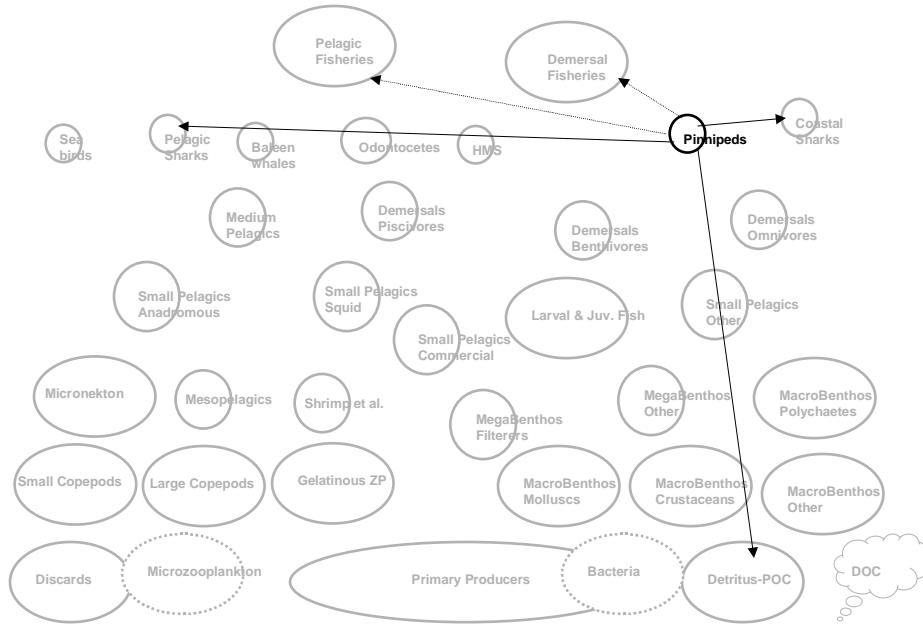
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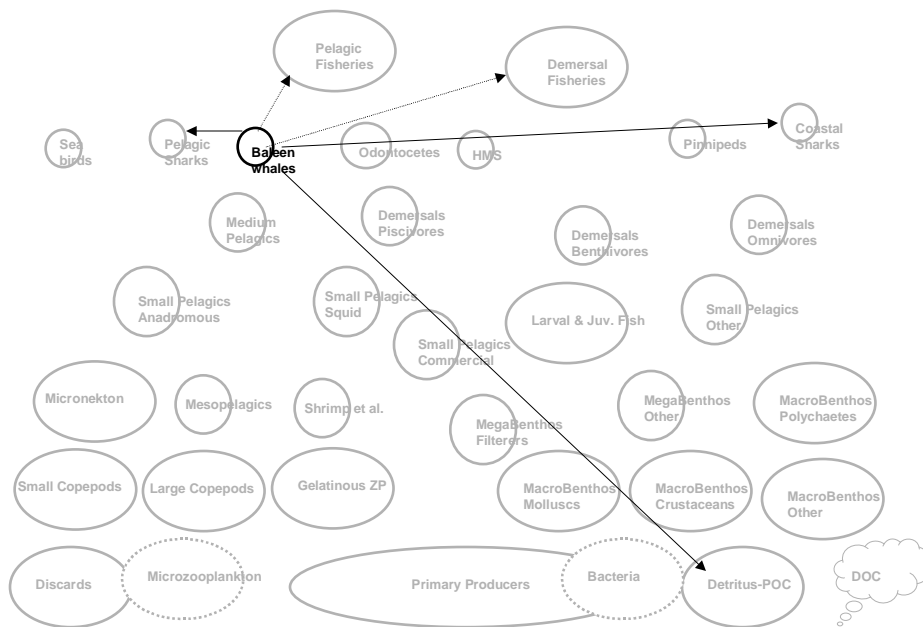
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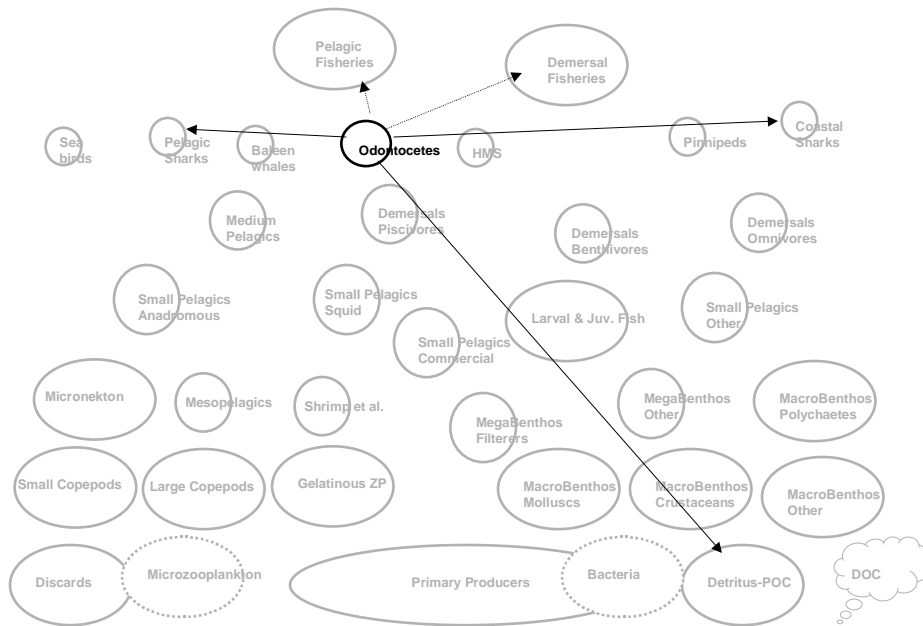
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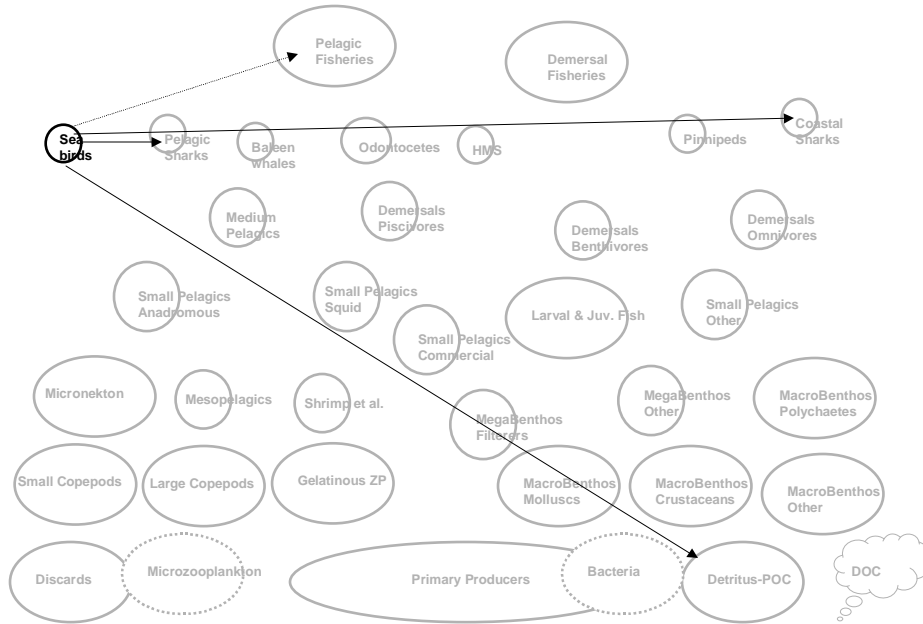
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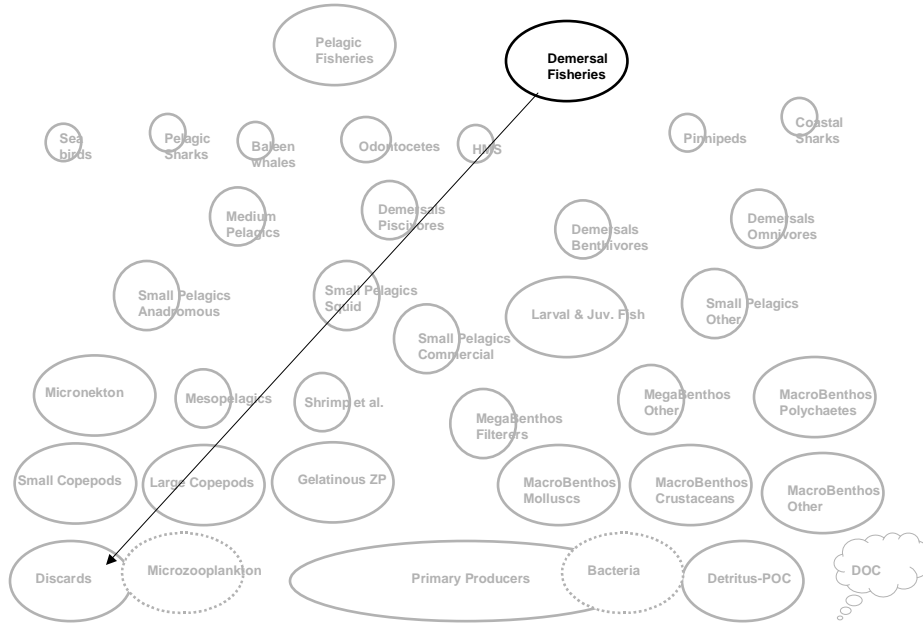
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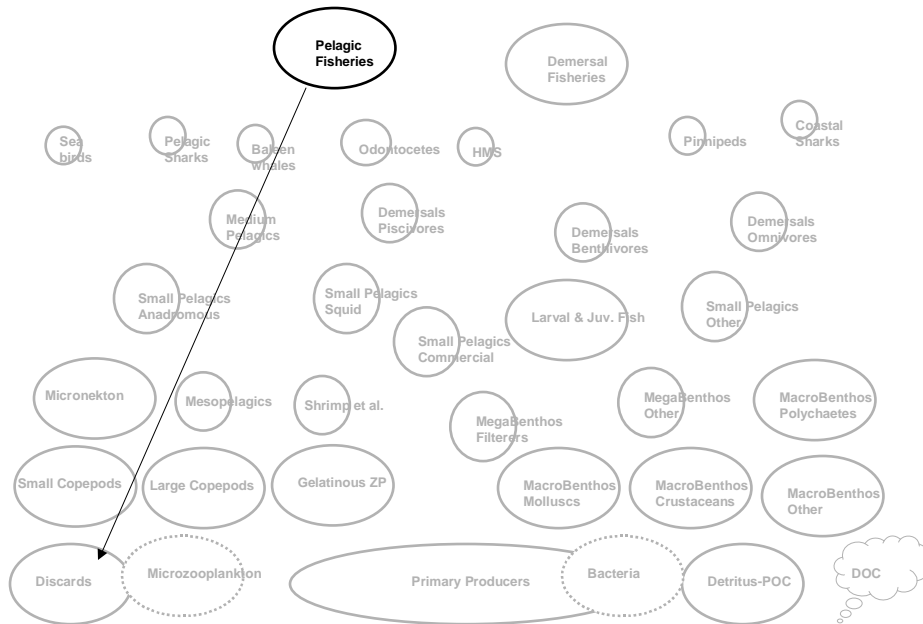
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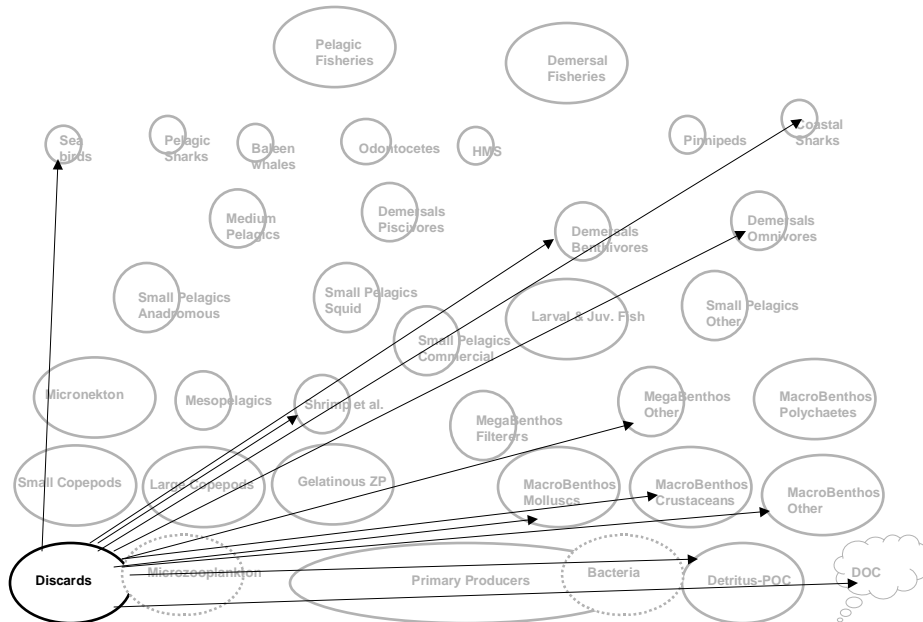
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EMAX



EMAX



23. Respiration

David Dow

Background and Approach

Two approaches were used to estimate metabolism in the EMAX project. Unless otherwise noted in each previous section, the default values for respiration were 65% of the assimilated consumption. Otherwise, where appropriate, values or formulae from the literature were used for the network nodes.

When appropriate literature values were lacking we assumed that assimilated energy was divided: 65% to respiration and 35% to secondary production (Parry 1983). The assimilated energy was estimated using the International Biological Program (IBP) approach where $C - E = \text{Assimilation} = P + R$. C represents consumption, E is egestion + excretion, P is secondary production and R represents respiration. There is a vast literature on the respiratory metabolism of individual organisms and many review papers with regressions or allometric equations which relate respiration to body size and temperature. Since field respiration values are influenced by feeding status, activity level, life history stage, body size, water temperature, etc., this extrapolation process generates a crude estimate. Since we did not have any respiration measurements for many of the nodes, and many of the nodes represent a composite of species, we decided to utilize this indirect approach to estimate the metabolic energy loss in most instances.

The EMAX network energy budget was interested in linking secondary production of the prey to either harvest or consumption by predators, so we did not focus on the metabolic energy losses from the system. The secondary production estimates were done independently and thus provided a reasonable estimate of the ecological transfer efficiency. Since the majority of the metabolic losses in the pelagic and benthic communities occur in the smaller size classes, this influences the base of the food web, leading to living marine resources (LMRs) and not the energy transfer efficiency within this chain.

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24. Model Protocols

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In this section we describe the software selection process, balancing exercises, diagnostics protocols and scenarios applied in the Energy Modeling and Analysis eXercise (EMAX).

A Primer on Energy Budgets and Network Models

Network models are based on the concept of a steady state ecosystem in which the energy inputs to a node are balanced by the outputs. Ecosystem network models trace the flows of energy or materials among compartments of the system. At steady state, the flows into a compartment exactly equal flows out of the compartment:

$$(EQ. 24.1) \quad \sum_{j=1}^n F_{ij} + I_i - \left(\sum_{j=1}^n F_{ji} + E_i \right) = 0$$

where F_{ij} is the flux from compartment j to compartment i ; I_i is import to compartment i from outside the system; and E_i is export from compartment i to outside the system. The estimates of production, consumption, and respiration described in earlier sections for each compartment are used in determining the flows among compartments. Under the assumption of steady-state conditions, these initial estimates of the flows are checked to see if the mass-balance criteria are met. If the system is not in steady-state, iterative adjustments are made to the flows in an attempt to achieve mass-balance.

Typically, all parameters necessary to determine the flows are not known and must be estimated. In general, there is not a unique solution to the system of linear equations (the problem is under-determined) and several alternative approaches were used to obtain solutions. We explored two alternative modeling approaches to examine solutions to this problem, the details of which are below.

Caveats and Assumptions

For the purposes of this exercise, we assumed steady state equilibrium. We acknowledge that there are dynamic elements of what we modeled, but averaging estimates over a five-year period mitigates some of the inter-annual dynamics.

For EMAX we assumed no movement of animals across regions (captured by proportionality of distributions spatially and seasonally). Thus, I_i was set to 0 and E_i was treated as fishery removals, bycatch, and ship-strikes for each appropriate node. That is, the network models didn't consider any potential transfer of matter or energy between the different subregions (Gulf of Maine; Georges Bank; Southern New England and Mid-Atlantic Bight) on the Northeast Continental Shelf, so that each system was treated in isolation.

We recognize the potential for a wide range of results depending upon which units are used. Although network models have been constructed using energy, biomass, or elemental units, we chose to execute our model in units of biomass (wet weight) per unit area.

Given that the carbon turnover of phytoplankton and bacteria is roughly 3 days, and that of fish varies over a range of 300 - 450 days (Hakanson and Gyllenhammar, 2005), it appears that the carbon formed in photosynthesis is recycled many times before reaching fish and marine mammals. This brings into question the assumption that this recycled carbon has the same qualitative value or embodied chemical energy at different trophic levels. Schneider and Sagan (2005) discuss the importance of distinguishing between carbon which cycles and energy which flows from sources to sinks. Direct carbon flow follows the pathways of energy, while the recycled carbon flow goes along the indirect pathways. It is important to distinguish between “cycles” (indirect flows) and “network connections” (direct flows) in carbon-based networks.

In classical energy flow models where joules or kilocalories are the measure of exchange between compartments, energy flows from sources (sunlight and resultant primary production) to sinks (higher trophic levels) with a large respiratory dissipation of energy at each trophic level. This highlights the need to resolve the apparent paradox between nutrients which cycle throughout the nodes within a network and energy which flows from sources to sinks with a large respiratory tax at each trophic level. In most network models, recycled energy is implicitly modeled as flows through indirect pathways.

The EMAX network budget was based on wet weight which lies at an intermediate point on the gradient between budgets based on carbon (which explicitly consider turnover time differences between compartments) and the classical energy flow budgets (J or kcal transported from sources to sinks).

Software and Modeling Approaches

We explored a broad selection of energy budget models, network models, and associated software packages for use in EMAX.

First we examined EcoNetwrk and constructed a preliminary model for the Gulf of Maine region. This approach uses reconstructed flows as the state variables (see Ulanowicz 2004 for an overview). Balancing the network proved to be challenging, as this model balances mainly by constraining respiration and consumption, and is a statistical minimization rather than a true optimization solution. Assumptions about primary production and detrital processing were key. We also explored Netwrk, the precursor to EcoNetwrk, which we decided was not likely to be an improvement over EcoNetwrk, particularly because it did not reside in a graphical user interface (GUI) environment.

We also constructed a preliminary model for Ecopath. This approach uses estimates of standing stocks as the state variables (see Christensen and Pauly 1992, Walters *et al.* 1997). Although initial balance was achieved, we were uncertain how much was due to detritus. This model balances primarily off ecotrophic efficiencies and uses a true optimization protocol.

Other software packages we investigated were WAND, WAND Balance, DR. LOOP, and SIMULLOOP. They may be useful for additional analyses once balanced budgets are formed using the two primary software packages, because they feature some useful cybernetic metrics. However, they are not likely to provide a balancing package of any improvement over the first two programs. Many packages provide useful information and analytical capabilities, but are not readily amenable for balancing a budget or easily translatable into the fisheries management context. Other models we evaluated as potentially very useful but rejected were redundant; focused on more qualitative network properties; were less user-friendly; or obfuscated their underlying model structure.

We also noted the potential for using some of the outputs from a concurrent GLOBEC Phase IV project, which could provide some MATLAB software to conduct energy budget balancing. Additionally, we made explorations into AD Model Builder and At-Risk/Excel, tools used to build models from scratch. Neither option, however, could be implemented in a timely manner.

After several iterations, we settled on using EcoPath (Christensen and Pauly 1992; Walters *et al.* 1997) and EcoNetwrk (Ulanowicz and Kay 1991; Ulanowicz 2004) as our primary tools. The pros and cons of each have been noted elsewhere (e.g., Walters *et al.* 1997; Heymans and Baird 2000; Hollowed *et al.* 2000; Whipple *et al.* 2000; Allesina and Bondavalli 2003; Kavanagh *et al.* 2004; Ulanowicz 2004). There is a subtle difference in the underlying philosophy and numerical solutions between the two programs (Heymans and Baird 2000).

The production (flows) for the heterotrophic compartments in EcoNetwrk can be expressed as:

$$(EQ. 24.2) \quad P = C - R - E$$

where P is production; C is consumption; R is respiration; and E is egestion (unassimilated food). The autotrophic compartment(s) considers respiration losses to gross primary production (GPP) to yield net primary production. Fishery yields are treated as exports from the system.

The mass balance EcoPath model can be expressed as:

$$(EQ. 24.3) \quad B_i (P/B)_i EE_i = C_i + \sum_j B_j (Q/B)_j DC_{ij}$$

where B_i is the biomass in the compartment; $(P/B)_i$ is the production to biomass ratio; EE_i is the ecotrophic efficiency (fraction of total production consumed by predators or exported from the system); C_i is the catch for compartment i ; B_j is the biomass for predator j ; $(Q/B)_j$ is the consumption to biomass ratio for predator j ; and DC_{ij} is the diet composition of predator j (fraction of biomass comprising prey i in the diet of predator j).

The benefit of using the two packages instead of choosing one is that their strengths and weaknesses can be played off against one another. The detritus box is the main weakness of Ecopath, while in EcoNetwrk it is egestion. Ecopath is an optimization program, whereas EcoNetwrk is a minimization procedure. These programs use two different methods to arrive at working, balanced solutions: Ecopath emphasizes P, while EcoNetwrk emphasizes R. Both use convergence of values with repeated (auto) balancing as the main way to verify model finalization. Even though the two models have a conceptually different approach (Ecopath is more top-down while EcoNetwrk is more bottom-up), both have highlighted the same deficiencies in our data matrix. A positive outcome of using both software packages is that we improve our input data and systemic understanding more than we would have by changing the model parameters using only one package. This also suggests that our results are robust to model choice.

Balancing Protocols

We made an initial calculation of the difference between the inflows and outflows from each compartment according to the specification of the input variables. For compartments exhibiting large discrepancies, we reexamined the input information for consistency, made

comparisons with similar inputs from other systems, and made adjustments as necessary. We then employed balancing options in both software packages to provide estimates of the steady-state flows. EcoNetwrk employs a manual balancing procedure in which an extended matrix comprising elements for the exchanges among compartments, respiration, imports, and exports is adjusted using successive transformations of this structural matrix (see Allesina and Bondavalli 2003). EcoNetwrk allows for “locking” estimates thought to be well determined and therefore provides an implicit weighting procedure. EcoPath employs a statistical balancing procedure using Singular Value Decomposition to constrain the estimates for the underdetermined system of equations. EcoPath allows the specification of an index of reliability (or “pedigree”) for each element to provide weighting options for estimation. Following each balancing procedure, we reevaluated inputs showing large deviations from mass balance or unrealistic estimates for certain diagnostic measures such as the ratio of production to consumption and respiration to consumption in EcoNetwrk, and the ecotrophic efficiency in EcoPath. Adjustments were made to the inputs to obtain more realistic estimates and the balancing protocols were repeated until stable estimates were obtained.

One of the benefits of this exercise and approach is that we identified major information/data gaps for the GOM (and generally NEUS) ecosystem (Table 24.1).

Ecopath Considerations

For the EcoPath model we initially investigated entering uncertainties globally rather than using the pedigree of data option on individual nodes. We used a 50% coefficient of variation (CV) on diet and Q:B values, and a 10% CV on biomass and P:B values.

The EcoPath model provided a range of options for autobalancing based either on minimizing maximum ecotrophic efficiencies, minimizing the sum of excess EEs, or minimizing the current EE. We chose the first two options simultaneously. Additionally, we used the Ecopath pedigree table to set confidence values for biomass, P:B, Q:B, diet and catch for autobalancing (Table 24.1). After examining several runs, the group decided that the pedigree approach was more desirable since it provided a way to weight the data sources with their relative degree of confidence.

Next, we began an iterative process whereby we modified the input/initial matrix and attempted to rebalance the network, primarily keying off $EE < 1$. For the initial Ecopath runs, P:C anomalies ($P:C > 0.5$) appeared to be the result of low consumption values rather than high production values. Using autobalancing based on ecotrophic efficiencies (EEs) worked well without causing major changes to network structure.

Large-scale changes were necessary to for gelatinous zooplankton, squid, demersal omnivores, macrobenthos - other, and shrimp. We reduced the C:B ratio, diet composition, and B for gelatinous zooplankton; C:B and P:B of demersal omnivores; C:B of macrobenthos mollusks; B and C:B of macrobenthos – other; diet composition of predators of small pelagics; and P:B and B of shrimp.

Since the balancing approach was iterative, we had to ask: When do we have a balanced model? The model was considered sufficiently balanced when we reran it starting at the solution and verified that it provided the same solution, conditioned upon minimizing EE via several numerical solution methodologies.

EcoNetwrk Considerations

For the EcoNetwrk model, we used an iterative approach similar to the one used for Ecopath. Repeated use of the balancing protocol (DATBAL, similar to AUTOBAL in Ecopath) was required to find a more global solution that would be responsive to input parameter changes.

The major consideration was to “close the loop” in EcoNetwrk by ensuring that the detrital node received unassimilated consumption from the other nodes in the network. We took the unassimilated fractions of all the consumptive flows (portions relegated to detritus), summed them and made microbial respiration equal to that sum. We also added 15% of primary production (phytoplankton direct contribution to detritus) to that sum to account for that flow, and the model then seemed to be more solvable.

Once these solutions were implemented, we carried out an iterative balancing process. For this we modified the input data matrix and attempted to rebalance the network primarily by keying off the R:C ratio. As a caveat, biomasses and C:B ratios seemed reasonable, but assimilation efficiencies (AE) were all >0.9. Again, the R:C ratio was a useful constraint in solving these multiple concerns.

Significant changes to gelatinous zooplankton (B, C:B); macrobenthos - other (B, R:B, C:B); larval fish (B); and shrimp (B, C:B, R:B) were initially required before we even came close to achieving network balance. These are similar to network nodes requiring similar changes in the EcoPath model version, our prebalance, and are noted as groups with lower data certainty (Table 24.1). We then modified megabenthos filterers, macrobenthos mollusks, medium pelagics, demersal omnivores, small pelagics anadromous, and small copepods.

Diagnostics

The input matrices and some diagnostic measures we used are provided in Appendix 1. Foremost is that once we identified a major constraining factor based upon the underlying assumption of the model software (i.e., EE or R:C), other key ratios were then examined. These model outputs must make sense relative to expert knowledge among EMAX personnel, and be consistent with literature values. In this way our exercise was unique; the large amount of extant, reasonable quality data allowed for a model reality check.

Many of these diagnostics (e.g., mean trophic level, ascendancy, input-output analysis, size spectra metrics, imbalance sum, pyramidal structure, connectance, etc.) might form the basis for indicators to be translated and incorporated into ecosystem approaches to fisheries management.

Scenarios

Once a balanced, baseline model was obtained for both software packages, various changes were made to the network (e.g., multiplying key nodes by various scalars such as $1/100^{\text{th}}$, $1/2$, 10, 100, singularly and in various combinations), which was then rebalanced. Although we have preliminary balanced networks for all four subregions, we chose to initially evaluate the various scenarios for only one of them, the Gulf of Maine. We executed the scenario rebalancing as a pseudo-dynamic modeling process to see where the perturbed system would redistribute biomass and production after the changes were imposed. We executed all scenarios in both model packages.

For comparisons across regions and across scenarios, we examined a set of network, cybernetic, and ecological statistics common to both software packages. However, to highlight the role of small pelagics in particular, we primarily evaluated a set of biomass ratios and similar indicators (Link 2005).

The bulk of the results and interpretation of these (and other) scenarios and the model balancing exercise are intended for presentation in other venues, but the main highlights are:

- Overall changes to major fish groups resulted in compensating changes to other fishes.
- The upper trophic levels (TLs) had minimal impact on the rest of the network.
- Changes to marine mammals sometimes had a counterintuitive effect on fish.
- Categorically across all scenarios, gelatinous zooplankton and macrobenthos decreased whereas most other zooplankton increased. Could that be a possible hardwiring artifact of the network structure?
- In terms of biomass, production, energy flows, and importance for upper trophic levels, small pelagics are a keystone group in this ecosystem.

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Table 24.1. Data pedigree for all nodes modeled in EMAX. Lower numbers or bluer colors are less certain/resolved estimates, and higher numbers or redder colors are more confident estimates (modified from a similar Ecopath module). B = Biomass, P:B = production, Q:B = consumption, Diet = diet composition, Catch = landed removals.

Group	B	P:B	Q:B	Diet	Catch	
Phytoplankton - primary producers	5	5	---	---	---	
Bacteria	2	2	2	2	---	Worse
Microzooplankton	2	2	2	2	---	
Small Copepods	4	3	3	2	---	
Large Copepods	4	3	3	2	---	
Gelatinous Zooplankton	3	2	2	2	0	
Micronekton	3	2	2	2	---	
Mesopelagics	3	2	2	3	---	
Macrobenthos - polychaetes	4	3	3	2	0	
Macrobenthos - crustaceans	4	3	3	2	0	
Macrobenthos - molluscs	4	3	3	2	0	
Macrobenthos - other	4	3	3	2	0	
Megabenthos - filterers	4	3	3	2	4	
Megabenthos - other	3	3	3	2	4	
Shrimp <i>et al.</i>	5	3	3	2	5	
Larval and juvenile fish	3	2	2	3	0	
Small Pelagics - commercial	5	7	7	5	5	
Small Pelagics - other	4	5	5	4	3	
Small Pelagics - squid	4	5	5	4	5	
Small Pelagics - anadromous	4	5	5	4	4	
Medium Pelagics (piscivores and other)	4	5	5	5	5	
Demersals - benthivores	5	5	7	5	5	
Demersals - omnivores	5	5	7	5	5	
Demersals - piscivores	5	5	7	5	5	
Sharks - pelagics	3	4	4	4	3	
Sharks - coastal	3	4	4	4	3	
HMS (highly migratory species)	3	6	4	4	3	
Pinnipeds	4	3	3	3	3	
Baleen Whales	4	3	3	3	3	
Odontocetes	4	3	3	3	---	
Sea Birds	4	3	3	4	---	
Fisheries - demersal	---	---	---	---	3	
Fisheries - pelagic	---	---	---	---	3	
Discards	---	---	---	---	3	
Detritus - POC	2	1	1	1	1	
DOC	2	1	1	1	1	

25. Discussion

The EMAX exercise and process of model balancing were informative in many respects. Paramount was highlighting areas where our perceptions or understanding may merit revision or reexamination in light of this holistic view of the data, relative magnitudes of different nodes, or combined model outputs.

Answering the Original Question- Evaluating the Role of Small Pelagics

Specific question:

What is the role of small pelagic fish in the Northeast United States (NEUS) Continental Shelf Ecosystem, as determined by a recent network analysis?

Answer:

Small pelagics are an extremely important part of the NEUS Ecosystem, and it is likely that they will continue to be for the foreseeable future. A majority of energy in the system flows through these nodes (commercial, squid, anadromous and other). An increasingly important issue is how other species, especially commercially or ecologically important ones, respond to herring, mackerel, squid, and similar organisms. It appears that when the amount of small pelagics in the system changes, there are trickle-through effects to other network nodes. In terms of biomass, production, energy flows, and importance for upper trophic levels, small pelagics are a keystone group of species in this ecosystem.

Overall, the pelagic community is more prominent than the benthic community. More fluxes pass through pelagic nodes than benthic or demersal ones. In particular, consumptive demand (C:P) is quite high for small pelagics, which indicate that these are keystone species groups.

Summary of Other Results

Total system production is less than primary production when one accounts for respiration, trophic transfer efficiencies, etc. This leads to the question of whether we have optimized biomass for all groups simultaneously. This is a key question for global fisheries management and should be addressed in additional exercises.

The system appears to be driven more from bottom-up than top-down factors. The NEUS Ecosystem is one of the most productive marine ecosystems on the planet, and that assessment is reinforced by this study. As a proportion of primary production, most of the events at upper trophic levels (particularly fisheries catches) are an extremely small fraction. More telling is that total fisheries catch is a low proportion of overall energy flow. Even when we increase the biomass of small pelagics by two orders of magnitude, the effects on the next lower trophic level down (zooplankton) are minimal. Further, given the connectedness of all the species in this ecosystem, it appears that if one energy pathway is altered, another pathway compensates such that overall changes in standing stock biomass at a given trophic level are minimized. These are all symptomatic of a highly productive and highly resilient system.

Overall, we found that lower trophic levels can be important in balancing energy fluxes. Despite uncertainties in some biomasses and rates, it appeared that dissolved organic carbon was the largest biomass node in the ecosystem by several orders of magnitude.

In balancing the network models, we found that it was necessary to add nodes for bacteria and microzooplankton to “close the loop”, be more realistic, recognize current scientific developments, and resolve the model. In this case, the additional metabolic energy fluxes due to including these nodes allowed for a realistic accounting of energy flows to detritus which can otherwise present challenges for balancing models. This represents a major change in thinking and philosophy of how the oceans work compared with even 10 to 20 years ago. Our observations suggest that bacteria may be very important for the NEUS Ecosystem. Finally, although we added detrital respiration along with the bacteria, we recognize that this may need to be modified in future investigations

Overall, there are minimal differences between the 4 main ecoregions. Generally speaking, marine mammals are less prominent in the more southerly regions. Similarly, small pelagics are important (more prominent, higher standing B, etc.) in the Gulf of Maine. Conversely, benthos are more prominent (in terms of overall system functioning) in the southerly regions.

We recognized that biomasses of some groups are inherently uncertain and will likely remain so. We also acknowledged that there was a large degree of amalgamation within network nodes. Yet tradeoffs in taxonomic accuracy versus system-wide generality need to be made.

It would be highly desirable to verify and refine our conversion factors for biomass to carbon across species groups, as most other marine networks deal in units of carbon. Similarly, our approach to approximating population rates varied across groups, but represented an attempt to balance prior knowledge and reasonableness of model outputs. Overall, the network analyses could be improved by enhanced knowledge of P:B and C:B ratios, and of appropriate conversion factors.

It was apparent that there is an enormous amount of information available at the NEFSC. The EMAX analyses described in this report started where a lot of other investigations have ended. For example, we did not attempt to reestimate a large number of parameters when balancing the network models, since we had empirical estimates of many parameters, particularly biomasses. Instead, we used input parameter estimates for biomasses, consumption to biomass ratios, and other parameters as consistency checks. This approach differs from how many other energy budget investigations with fewer data have been conducted.

Data Gaps

One fundamental observation is that considerable data gaps exist for a variety of ecosystem components and processes necessary for EMAX modeling. Even in data rich systems there are still gaps (Table 24.1). This is not surprising given the complexity of the NEUS Ecosystem and the difficulties in sampling multiple spatial scales and marine habitats. Although data gaps were generally addressed by using the best available information from the literature, the limited empirical information on key vital rates, biomass estimates for some nodes, and most diet compositions was considered to be especially important for improving our understanding of the ecosystem.

Many of the key rate parameters necessary for understanding how marine ecosystems function are not well known. Even for the better-studied components of the food web (i.e., fish

and marine mammals), population rates such as production, consumption and respiration are not commonly estimated. As a result, our EMAX analyses relied on literature values or simple approximations for many species groups. Imputting such rates created the danger of propagating potential errors from past studies, as well as not accounting for potential changes through time. We recommend a suite of process-oriented studies and complementary laboratory work to directly estimate production, consumption, and respiration rates for the individual species and species groups examined.

Another primary data gap was the lack of direct estimates of standing stock biomass for several groups of species. In particular, the biomasses of the following species groups were not well known: mesopelagic fishes*, macro- and mega-benthos*, micronekton, shrimp*, bacteria, microzooplankton, gelatinous zooplankton*, and larval fish*. For these species groups, we used historical estimates, expansion of density estimates taken from the literature, or expert opinion based on the relative abundances of other groups with biomass estimates. Several of these groups are very difficult to sample using existing technologies (e.g., micronekton, bacteria, and microzooplankton). Biomasses of the other groups, however, could probably be estimated if modified sampling gears or technologies were deployed in research surveys (* in list above). Regardless, the biomasses of these groups warrant further investigation, because they consistently emerge as pivotal species groups in modeling energy fluxes and balancing energy flows. For example, in one sensitivity analysis we found that a halving of the estimate of gelatinous zooplankton substantially altered the biomasses of other zooplankton, larval fish, and micronekton. These changes, in turn, transferred up the food web to affect commercially important and protected species groups.

Some species groups are always going to be problematic or inherently underdetermined. Until clear advances in sampling and monitoring technology are developed and become routine, we may have to simply recognize that many of our efforts for estimating parameters associated with these types of groups simply provide a bounding of possible magnitudes.

Diet composition of most species groups was limited, with the exception of mid-trophic level fishes which have been reasonably well sampled in this ecosystem. In particular, the feeding ecology of upper trophic level species warrants further investigation to characterize diet composition and consumption. Novel approaches to use sampling of isotopic signatures, fatty acids, protein structures, bioassays, etc., via tissue plugs can provide non-lethal means of assessing the diets of the larger, charismatic megafauna. Direct measurement of the feeding ecology of lower trophic level organisms (e.g., benthos, zooplankton) is also important and we recommend that research be conducted to improve the estimates of diet composition for these organisms. Even those species groups for which we have a relatively significant amount of information (e.g., demersal fishes), seasonal data collections of diet data would help to estimate energy fluxes among groups.

The effect of fisheries on the NEUS Ecosystem has been relatively well investigated through ongoing long-term fishery data collection programs. Nonetheless, an accurate accounting of fishery removals (both landings and discards) by location is needed to measure regional fisheries effects on ecosystem processes. Partitioning catches to area using current logbook and dealer data was complicated for some species. Creating a more spatially explicit reporting scheme for fisheries landings and discards in the NEUS Ecosystem would help to reduce uncertainty about estimates of regional fisheries effects.

Model Considerations

While estimating parameters of the network models, we found that diet composition and consumption rates were very important to achieving balanced energy budgets. In this context, getting the flows right is critical and it is important to iteratively refit the models to achieve balance. We also found that species groups with relatively small biomasses pose unique balancing problems.

Approximation or estimation approaches have varied, but literature ranges proved to be a helpful way to address and scale the magnitude of those estimates that were undetermined locally. There may be better ways to estimate many of our parameters, as the approaches we used often represent a compromise for the sake of simplicity.

We found that there was value in using multiple modeling approaches. While the differences among the software packages we examined were not trivial, the overall results were similar for the ones we used (Ecopath and EcoNetwrk). This concordance suggests that the underlying data, rather than the structural equations used in the particular models, had a dominant influence on the results.

Summary and Conclusions

Small pelagics clearly are and will likely remain a critical part of this ecosystem for the foreseeable future. Changes to the biomass and vital rates of these species could have major impacts on other components of the ecosystem. Currently, however, there does not appear to be a shortage of biomass of this group available for other groups. In addition, most small pelagic predators do have some capacity to switch prey. Thus, the strong trophic linkages seen in other ecosystems may not be of as much concern here.

Obviously there is a lot more we could elaborate on from this work. In particular, future efforts should initially consist of more detailed examinations of a broader set of cybernetic and systems metrics. Comparing the results of the contemporary study to some historical energy budgets from this region will also be valuable. Comparative studies exploring the differences and similarities across other marine ecosystems will better elucidate key marine and fisheries processes, patterns, and theories. We will also be able to even further elucidate the key dynamics of the ecosystem with further comparisons across the four ecoregions; more detailed analyses between the two (and perhaps other) model outputs; exploration of other statistics; and testing scenarios more rigorously and formally.

There is an ever-increasing need for holism in marine and fisheries science. One of the values of an exercise like this is gaining a better sense of the relativity of concurrent processes. That the dynamics of this and likely most marine ecosystems are dominated by the first two trophic levels is a sober reminder that the relative magnitude of important events and processes may often be beyond human control. Yet at the same time, our ability to even detect changes in network nodes that are often highly influenced by human events in marine systems (e.g., fishing) is critical. Being able to evaluate such events in the context of an entire system is going to be an increasingly important task as we move toward ecosystem-based fisheries management.

26. EMAX Glossary

Carolyn A. Griswold

Assimilation Efficiency (AE) - In an animal, the percentage of energy content of ingested food absorbed across the gut wall. In primary producers, the percentage of solar visible light fixed by photosynthesis.

Biomass (B) - Living weight, including stored food; the amount of living matter as in a unit area or volume of habitat. Measure of the quantity of a stock at a given time, usually by weight in pounds or metric tons (2,205 pounds = 1 metric ton).

Bycatch - Many fishers are catching more unwanted species, juveniles, and other marine wildlife than they intend. These non-target species are known as bycatch. Annually, 30 million metric tons - more than 25 per cent of all fish caught - is being thrown over the side of fishing boats, dead or dying.

Catch - Fishery removal which is considered fishing mortality. The catch can consist of targeted species and bycatch or discards.

Chlorophyll - Using satellite sensors, we can measure chlorophyll concentrations in oceans, lakes and seas to indicate the distribution and abundance of phytoplankton. Phytoplankton are the base of the marine food chain and, therefore, are a good indicator of the abundance of life in a body of water.

Consumption (C) - The process of taking food into an organism (eating, ingestion, intake, uptake, etc.). Reported as a rate.

Consumption:Biomass (C:B) - A ratio.

Consumption:Production (C:P) - A ratio.

Consumptive flows - The amount of biomass flowing into a network node from other sources (typically predation).

Consumptive removals - The sum of removals via predation from all sources.

Diet composition - Any matter or combination of matter ingested by an individual or defined group of organisms for any given time period. Usually expressed as a percentage.

Discards - The portion of a catch not used and thrown away at sea.

Dry weight (dw) – Mass of tissue minus the weight of free water.

Ecological efficiency - A mathematical statement of the ratio between the energy available to an organism or group or group processes, and the energy actually expended. A 10 % gain is average, 20 % is very good, and 5 % is typical of the top of the food chain.

Ecotrophic Efficiency (EE) - The fraction of production ($P = B \cdot [P:B]$) consumed or caught within the system (including net migration and biomass accumulation). EE can be for one species or a species guild.

Egestion - Expulsion of non-assimilated matter (excess and/or unused food) from the body.

Excretion - Discharge or elimination of an absorbed or endogenous substance or of a waste product, and/or their metabolites, through some tissue of the body and its appearance in urine, feces, or other products normally leaving the body. Also the act or process of discharging waste or other matter from the blood, tissues, or organs.

Fishery removal - The sum of fishing mortality. Added together with natural mortality, they equal total mortality.

Gross Growth Efficiency (GGE) - Secondary Production (P)/Consumption (C), where P is composed of growth + reproduction, while C is the food ingested. Consumption = Secondary Production (P) + Respiration (R) + Egestion (E). The EcoNetwrk program uses $P = \text{Production} + \text{Egestion (E)}$, where E represents unassimilated consumption, which is an important parameter in Ecopath with Ecosim (EwE). P:C is sometimes referred to as k_1 .

Gross primary production/productivity - The total amount of organic matter produced by autotrophs.

Gross production - The total rate of photosynthesis including the organic matter used up in respiration during the measurement period. This is also known as total photosynthesis or total assimilation and can be expressed as $\text{g C m}^{-2} \text{ day}^{-1}$.

Growth - A change in size over time (a rate). A value is obtained by dividing the change by the period of time elapsed during the change.

Input – In the model, parameters (C:B, P:B, R:B, diet composition matrix, etc.) or external forcing used to initialize the model.

Interaction matrix - A table in which the cell elements are rankings. In the context of a fisheries ecosystem, the table would indicate who ate whom.

Landings - The amount of fish or shellfish by weight (expressed as live weight or equivalents) that is brought ashore (or to a factory ship), usually for sale. Nominal catches do not include unreported discards.

Mass balance - These equations are based on an assumption of steady state equilibrium of biomass, and formulate that for any given group its production can be described as:

$$\begin{aligned} \text{Production} &= \text{Catches} + \text{Predation} + \text{Biomass Accumulation} \\ &\quad + \text{Net Migration} + \text{Other Mortality} \end{aligned}$$

And further, that

$$\text{Consumption} = \text{Production} + \text{Unassimilated Food} + \text{Respiration}$$

At steady state (EMAX), the consumptive flows = productive flows. Ecopath can be operated in a non-steady state mode which allows biomass to accumulate in a compartment. Since Ecopath is not a dynamic simulation model, it provides a static picture of the biomass and flows within the ecosystem at one point in time (usually yearly average).

Net Growth Efficiency (NGE) - Secondary Production (P)/Assimilation (A), where $A = C - E$ or $C \times \text{Assimilation Efficiency (AE)} = A$. Assimilated energy is composed of P + R (Respiration). P:A is sometimes referred to as k2.

Net production - The amount of organic matter produced by plants and remaining after subtracting the matter consumed by respiration.

Other removals - The amount of biomass removed from other sources. In EMAX this refers to ship strikes of large marine mammals.

Output - Generated by the model and can be either biotic or abiotic. This information is used to evaluate model performance, network balance, and scenario outcome.

Primary production/productivity - The photosynthesis and production of organic matter by plants from inorganic material and sunlight energy.

Net primary production/productivity - The energy remaining after respiratory needs have been met, i.e., Net Primary Production = Gross Primary Production – Respiration, expressed as grams of carbon fixed per square meter of sea surface per unit of time.

Production:biomass (P:B) - A ratio.

Production:respiration (P:R) - A ratio.

Productive flows - The allocation of biological production from one compartment to a set of recipient compartments.

Reproduction - The process by which a new organism is produced.

Respiration (R) - The bodily processes involved in exchange of oxygen and carbon dioxide between an organism and the environment.

Respiration:biomass (R:B) - A ratio.

Respiration:consumption (R:C) - A ratio.

Sloppy feeding - Loss of material due to inefficient feeding. For example, when prey is large relative to a copepod (e.g., during a bloom of large cells), copepods are not an efficient link to higher trophic levels. They lose significant amounts of what they clear to the surroundings as dissolved material (DOC).

Total production (P) - The total amount of biomass produced, including any respiratory losses.

Transfer efficiency - The fraction of energy that is usefully transferred, usually expressed as a percentage.

Wet weight (ww) – Mass of tissue including water content.

27. Appendix A – Preliminary Networks for Each Region

Mid-Atlantic Bight network input data.

Units for Biomass are in g m^{-2} ; units for Production, Bycatch, Targeted Fishery/Navigation Removals, Consumption and Respiration are in $\text{g m}^{-2} \text{yr}^{-1}$.

Taxa	Biomass	Production	P/B	Bycatch	Targeted Fishery/Navigation Removals	Consumption	C/B	Assimilation Efficiency	Unassimilated Consumption	Respiration	R/B	C/P	P/R	R/C	Living or Dead
Phytoplankton - Primary Producers	20.0455	4251.874	212.11	0	0	0	0	1	0	1062.968	53.03	0	4.00	0	L
Bacteria	4.47320	408.1799	91.25	0	0	1700.749	380.21	0.8	0.2	952.4196	212.92	4.17	0.43	0.56	L
Microzooplankton	3.14724	226.6013	72.00	0	0	762.9673	242.42	0.9	0.1	460.0693	146.18	3.37	0.49	0.60	L
Small Copepods	3.70002	246.16771	66.53	0	0	472.67710	127.75	0.75	0.25	230.43009	62.28	1.92	1.07	0.49	L
Large Copepods	5.22595	395.40245	75.66	0	0	572.24194	109.5	0.75	0.25	278.96794	53.38	1.45	1.42	0.49	L
Gelatinous Zooplankton	3.63489	145.39579	40	8.413E-07	0	530.69462	146	0.65	0.35	224.21848	61.69	3.65	0.65	0.42	L
Micronekton	5.88884	83.91603	14.25	0.00938	0	854.18267	145.05	0.75	0.25	416.41405	70.71	10.18	0.20	0.49	L
Mesopelagics	0.00230	0.00219	0.95	2.302E-10	0	0.00420	1.83	0.85	0.15	0.00232	1.01	1.92	0.94	0.55	L
Macrobenthos - polychaetes	12.39897	30.99743	2.5	0.00012	0	216.98203	17.5	0.5	0.5	70.51916	5.69	7	0.44	0.33	L
Macrobenthos - crustaceans	3.28887	9.86661	3	3.289E-05	0	69.06628	21	0.5	0.5	22.44654	6.83	7	0.44	0.33	L
Macrobenthos - molluscs	15.57963	31.15926	2	0.00066	0	218.11480	14	0.4	0.6	56.70985	3.64	7	0.55	0.26	L
Macrobenthos - other	94.51230	189.02460	2	0.00095	0	1701.22140	18	0.5	0.5	552.89695	5.85	9	0.34	0.33	L
Megabenthos - filterers	3.63356	30.58	8.42	0.90612	2.97168	36.33555	10	0.3	0.7	7.08543	1.95	1.19	4.32	0.20	L
Megabenthos - other	6.53196	13.04217	2.00	0.00876	0.01438	117.57522	18	0.7	0.3	53.49673	8.19	9.02	0.24	0.46	L
Shrimp <i>et al.</i>	0.06177	0.06177	1	0.00938	0.03001	0.55589	9	0.7	0.3	0.25293	4.10	9	0.24	0.46	L
Larval and Juvenile Fish - all	0.51699	10.85677	21	5.315E-09	0	23.26451	45	0.85	0.15	12.85364	24.86	2.14	0.84	0.55	L
Small Pelagics - commercial	5.99848	2.21717	0.37	0.04882	0.18008	11.99695	2	0.85	0.15	6.62832	1.11	5.41	0.33	0.55	L
Small Pelagics - other	3.92701	3.73214	0.95	0.09290	0.91578	7.85402	2	0.65	0.35	3.31832	0.85	2.10	1.12	0.42	L
Small Pelagics - squid	1.42474	1.35404	0.95	0.00232	0.02303	3.91804	2.75	0.85	0.15	2.16472	1.52	2.89	0.63	0.55	L
Small Pelagics - anadromous	0.11205	0.04762	0.42	0.02252	0.20916	0.22409	2	0.85	0.15	0.12381	1.11	4.71	0.38	0.55	L
Medium Pelagics - piscivores & other	0.90758	0.40841	0.45	0.01849	0.05935	1.85147	2.04	0.85	0.15	1.02294	1.13	4.53	0.40	0.55	L
Demersals - benthivores	5.50998	2.47949	0.45	0.01228	0.03232	3.48782	0.63	0.7	0.3	1.58696	0.29	1.41	1.56	0.46	L
Demersals - omnivores	1.49980	0.67491	0.45	0.01840	0.02810	1.19984	0.8	0.65	0.35	0.50693	0.34	1.78	1.33	0.42	L
Demersals - piscivores	6.28162	2.82673	0.45	0.10683	0.35609	7.22387	1.15	0.85	0.15	3.99119	0.64	2.56	0.71	0.55	L
Sharks - coastal	0.01699	0.00170	0.1	0.00732	0.02441	0.02480	1.46	0.85	0.15	0.01370	0.81	14.6	0.12	0.55	L
Sharks - pelagics	0.01024	0.00102	0.1	0.00031	0.00104	0.01351	1.32	0.85	0.15	0.00747	0.73	13.20	0.14	0.55	L
Highly Migratory Species	0.00875	0.00437	0.50	0.00305	0.01015	0.07219	8.25	0.85	0.15	0.03989	4.56	16.53	0.11	0.55	L
Baleen Whales	0.16264	0.00619	0.04	8.814E-09	0.00085	0.67494	4.15	0.8	0.2	4.23712	26.05	109.07	0.00	6.28	L
Odontocetes	0.03289	0.00132	0.04	1.284E-08	0	0.57102	17.36	0.8	0.2	0.52920	16.09	434	0.00	0.93	L
Sea Birds	0.00363	0.00100	0.28	3.634E-05	0	0.06303	17.34	0.85	0.15	0.03482	9.58	63.06	0.03	0.55	L
Discards	1.26865	N/A	-	0	0	-	-	-	-	-	-	-	-	-	D
Detritus - POC	30	4251.87356	-	0	0	-	-	-	-	-	-	-	-	-	D

Southern New England network input data.

Units for Biomass are in g m⁻²; units for Production, Bycatch, Targeted Fishery/Navigation Removals, Consumption and Respiration are in g m⁻² yr⁻¹.

Taxa	Biomass	Production	P/B	Bycatch	Targeted Fishery/Navigation Removals	Consumption	C/B	Assimilation Efficiency	Unassimilated Consumption	Respiration	R/B	C/P	P/R	R/C	Living or Dead
Phytoplankton - Primary Producers	20.47293	3743.666	182.86	0	0	0	0	1	0	935.9165	45.71	0	4	0	L
Bacteria	3.93854	359.392	91.25	0	0	1497.466	380.21	0.8	0.2	838.5813	212.92	4.17	0.43	0.56	L
Microzooplankton	3.21435	231.433	72.00	0	0	779.2358	242.42	0.9	0.1	469.8792	146.18	3.37	0.49	0.60	L
Small Copepods	7.60227	345.38738	45.43	0	0	971.19054	127.75	0.75	0.25	473.45539	62.28	2.81	0.73	0.49	L
Large Copepods	11.53543	715.03955	61.99	0	0	1263.12976	109.5	0.75	0.25	615.77576	53.38	1.77	1.16	0.49	L
Gelatinous Zooplankton	3.88780	155.51200	40	6.359E-07	0	567.61880	146	0.65	0.35	239.81894	61.69	3.65	0.65	0.42	L
Micronekton	8.46559	120.63467	14.25	0.01	0	1179.14155	139.29	0.75	0.25	574.83151	67.90	9.77	0.21	0.49	L
Mesopelagics	0.00131	0.00125	0.95	1.314E-10	0	0.00240	1.83	0.85	0.15	0.00133	1.01	1.92	0.94	0.55	L
Macrobenthos - polychaetes	35.43624	88.59059	2.5	0.00	0	620.13416	17.5	0.5	0.5	201.54360	5.69	7	0.44	0.33	L
Macrobenthos - crustaceans	6.14084	18.42251	3	6.141E-05	0	128.95758	21	0.5	0.5	41.91122	6.83	7	0.44	0.33	L
Macrobenthos - molluscs	10.26354	20.52707	2	0.00	0	143.68949	14	0.4	0.6	37.35927	3.64	7	0.55	0.26	L
Macrobenthos - other	39.04129	78.08258	2	0.00	1.66837	702.74326	18	0.5	0.5	228.39156	5.85	9	0.34	0.33	L
Megabenthos - filterers	3.70247	31.16	8.42	0.52	0.15280	37.02471	10	0.3	0.7	7.21982	1.95	1.19	4.32	0.20	L
Megabenthos - other	4.49719	8.99438	2	0.05	0	80.94938	18	0.7	0.3	36.83197	8.19	9	0.24	0.46	L
Shrimp <i>et al.</i>	0.06782	0.06782	1	0.01	0.03076	0.61039	9	0.7	0.3	0.27773	4.10	9	0.24	0.46	L
Larval and Juvenile Fish - all	0.84448	17.73400	21	8.681E-09	0.44049	38.00143	45	0.85	0.15	20.99579	24.86	2.14	0.84	0.55	L
Small Pelagics - commercial	13.88781	5.04278	0.36	0.16	0.03046	27.77561	2	0.85	0.15	15.34603	1.11	5.51	0.33	0.55	L
Small Pelagics - other	1.15134	1.09421	0.95	0.03	0.00694	2.30268	2	0.65	0.35	0.97288	.85	2.10	1.12	0.42	L
Small Pelagics - squid	2.72805	2.59268	0.95	0.00	0.24766	7.50214	2.75	0.85	0.15	4.14493	1.52	2.89	0.63	0.55	L
Small Pelagics - anadromous	0.16034	0.06814	0.42	0.04	0.06459	0.32067	2	0.85	0.15	0.17717	1.11	4.71	0.38	0.55	L
Medium Pelagics - piscivores & other	0.20684	0.09308	0.45	0.02	0.08330	0.42195	2.04	0.85	0.15	0.23313	1.13	4.53	0.40	0.55	L
Demersals - benthivores	1.38310	0.62239	0.45	0.03	0.01460	0.87550	0.63	0.7	0.3	0.39835	0.29	1.41	1.56	0.46	L
Demersals - omnivores	2.48951	1.12028	0.45	0.01	0.29123	1.99161	0.8	0.65	0.35	0.84145	0.34	1.78	1.33	0.42	L
Demersals - piscivores	6.80530	3.06238	0.45	0.09	0.01214	7.82609	1.15	0.85	0.15	4.32392	0.64	2.56	0.71	0.55	L
Sharks - coastal	0.01586	0.00159	0.1	0.00	0.00115	0.02315	1.46	0.85	0.15	0.01279	0.81	14.6	0.12	0.55	L
Sharks - pelagics	0.01987	0.00199	0.1	0.00	0.00760	0.01351	0.68	0.85	0.15	0.00747	0.38	6.80	0.27	0.55	L
Highly Migratory Species	0.00990	0.00578	0.58	0.00	0	0.07219	7.29	0.85	0.15	0.03989	4.03	12.49	0.14	0.55	L
Pinnipeds	0.018	0.0019	.11	3.168E-11	0	0.158	8.78	0.8	0.2	1.17049	65.03	83.16	0.002	3.30	L
Baleen Whales	0.28580	0.01158	0.04	1.707E-08	0.00049	1.28326	4.49	0.8	0.2	4.23712	14.83	110.81	0.003	3.30	L
Odontocetes	0.05787	0.00231	0.04	1.306E-08	0	0.92360	15.96	0.8	0.2	0.52920	9.14	399	0.004	0.57	L
Sea Birds	0.00633	0.00174	0.28	6.334E-05	0	0.06303	9.95	0.85	0.15	0.03482	5.50	36.19	0.05	0.55	L
Discards	0.97425	N/A	-	0	0	-	-	-	-	-	-	-	-	-	D
Detritus - POC	40	3743.66606	-	0	0	-	-	-	-	-	-	-	-	-	D

Georges Bank network input data.

Units for Biomass are in g m^{-2} ; units for Production, Bycatch, Targeted Fishery/Navigation Removals, Consumption and Respiration are in $\text{g m}^{-2} \text{yr}^{-1}$.

Taxa	Biomass	Production	P/B	Bycatch	Targeted Fishery/Navigation Removals	Consumption	C/B	Assimilation Efficiency	Unassimilated Consumption	Respiration	R/B	C/P	P/R	R/C	Living or Dead
Phytoplankton - Primary Producers	19.77286	3284.948	166.13	0	0	0	0	1	0	821.2371	41.53	0	4.00	0	L
Bacteria	3.455946	315.355	91.25	0	0	1313.979	380.21	0.8	0.2	735.8284	212.92	4.17	0.43	0.56	L
Microzooplankton	3.104434	223.5193	72.00	0	0	752.5901	242.42	0.9	0.1	453.8118	146.18	3.37	0.49	0.60	L
Small Copepods	9.98857	416.17423	41.67	0	0	1276.04001	127.75	0.75	0.25	622.06950	62.28	3.07	0.67	0.49	L
Large Copepods	14.24652	778.37084	54.64	0	0	1559.99396	109.5	0.75	0.25	760.49705	53.38	2.00	1.02	0.49	L
Gelatinous Zooplankton	5.24931	209.97247	40	6.359E-07	0	766.39951	146	0.65	0.35	323.80379	61.69	3.65	0.65	0.42	L
Micronekton	7.61025	108.44609	14.25	0	0	277.77419	36.5	0.75	0.25	135.41492	17.79	2.56	0.80	0.49	L
Mesopelagics	0.00004	0.00003	0.95	3.664E-12	0	6.687E-05	1.83	0.85	0.15	3.695E-05	1.01	1.92	0.94	0.55	L
Macrobenthos - polychaetes	5.16706	12.91766	2.5	0.0	0	90.42362	17.5	0.5	0.5	29.38768	5.69	7	0.44	0.33	L
Macrobenthos - crustaceans	16.46480	49.39439	3	0.0	0	345.76073	21	0.5	0.5	112.37224	6.83	7	0.44	0.33	L
Macrobenthos - molluscs	2.57672	5.15343	2	0.0	0	36.07402	14	0.4	0.6	9.37925	3.64	7	0.55	0.26	L
Macrobenthos - other	81.67872	163.35744	2	0.0	0.64780	1470.21698	18	0.5	0.5	477.82052	5.85	9	0.34	0.33	L
Megabenthos - filterers	4.14449	34.88	8.42	0.2	0.03305	41.44487	10	0.3	0.7	8.08175	1.95	1.19	4.32	0.20	L
Megabenthos - other	4.36	8.72	2	0.0	0	78.48	18	0.7	0.3	35.7084	8.19	9	0.24	0.46	L
Shrimp <i>et al.</i>	0.00010	0.0001	1	0.0	0.00023	0.0009	9	0.7	0.3	0.00041	4.10	9	0.24	0.46	L
Larval and Juvenile Fish - all	0.46715	7.00728	15	4.802E-09	0.29900	21.02185	45	0.85	0.15	11.61457	24.86	3	0.60	0.55	L
Small Pelagics - commercial	9.94662	3.43428	0.35	0.02990	0	19.89325	2	0.85	0.15	10.99102	1.11	5.79	0.31	0.55	L
Small Pelagics - other	1.05437	1.00205	0.95	0	0.00339	2.10874	2	0.65	0.35	0.89094	0.85	2.10	1.12	0.42	L
Small Pelagics - squid	0.96230	0.91455	0.95	0.00034	0.03276	2.64633	2.75	0.85	0.15	1.46210	1.52	2.89	0.63	0.55	L
Small Pelagics - anadromous	0.03775	0.01604	0.42	0.00328	0.01015	0.07551	2	0.85	0.15	0.04172	1.11	4.71	0.38	0.55	L
Medium Pelagics- piscivores & other	0.19284	0.08678	0.45	0.00305	0.26416	0.46861	2.43	0.85	0.15	0.25891	1.34	5.4	0.34	0.55	L
Demersals - benthivores	5.01958	2.25881	0.45	0.07925	0.00531	4.61801	0.92	0.7	0.3	2.10120	0.42	2.04	1.08	0.46	L
Demersals - omnivores	3.77876	1.70044	0.45	0.00159	0.53144	3.13637	0.83	0.65	0.35	1.32512	0.35	1.84	1.28	0.42	L
Demersals - piscivores	4.25437	1.91447	0.45	0.15943	0	10.38066	2.44	0.85	0.15	5.73532	1.35	5.42	0.33	0.55	L
Sharks - pelagics	0.02436	0.00244	0.1	0.00024	0.00341	0.01351	0.55	0.85	0.15	0.00747	0.31	5.55	0.33	0.55	L
Highly Migratory Species	0.03516	0.02400	0.68	0.00102	0	0.07219	2.05	0.85	0.15	0.03989	1.13	3.01	0.60	0.55	L
Baleen Whales	0.41672	0.01584	0.04	1.247E-08	0.00011	1.87523	4.5	0.8	0.2	0.97512	2.34	118.36	0.02	0.52	L
Odontocetes	0.12200	0.00488	0.04	1.019E-08	0	1.75675	14.4	0.8	0.2	0.91351	7.49	360	0.01	0.52	L
Sea Birds	0.01439	0.00396	0.28	0.00014	0	0.06303	4.38	0.85	0.15	0.03482	2.42	15.92	0.11	0.55	L
Discards	0.48364	N/A	-	-	-	-	-	-	-	-	-	-	-	-	D
Detritus - POC	50	821.23707	-	-	-	-	-	-	-	-	-	-	-	-	D

Gulf of Maine network input data.

Units for Biomass are in g m^{-2} ; units for Production, Bycatch, Targeted Fishery/Navigation Removals, Consumption and Respiration are in $\text{g m}^{-2} \text{yr}^{-1}$.

Taxa	Biomass	Production	P/B	Bycatch	Targeted Fishery/Navigation Removals	Consumption	C/B	Assimilation Efficiency	Unassimilated Consumption	Respiration	R/B	C/P	P/R	R/C	Living or Dead
Phytoplankton - Primary Producers	20.11436	3281.52067	163.14	0	0	0	0	1	0	820.3375	40.78	0	4.00	0	L
Bacteria	3.45234	315.026	91.25	0	0	1312.608	380.21	0.8	0.2	735.0607	212.92	4.17	0.43	0.56	L
Microzooplankton	3.15805	227.37972	72	0	0	765.58815	242.42	0.9	0.1	461.6497	146.18	3.37	0.49	0.60	L
Small Copepods	9.87932	305.44967	30.92	0	0	1262.08309	127.75	0.75	0.25	615.26550	62.28	4.13	0.50	0.49	L
Large Copepods	34.85446	1410.16647	40.46	0	0	3816.56345	109.5	0.75	0.25	1860.57469	53.38	2.71	0.76	0.49	L
Gelatinous Zooplankton	11	440	40	6.359E-07	6.359E-07	1610.14239	146	0.65	0.35	680.28516	61.84	3.66	0.65	0.42	L
Micronekton	8.35650	119.08006	14.25	0	0	305.01207	36.5	0.75	0.25	148.69338	17.79	2.56	0.80	0.49	L
Macrobenthos - polychaetes	13.49161	33.72902	2.5	6.824E-12	0.00013	236.10311	17.5	0.5	0.5	76.73351	5.69	7	0.44	0.33	L
Macrobenthos - crustaceans	1.83497	5.50491	3	0.00013	1.835E-05	38.53436	21	0.5	0.5	12.52367	6.83	7	0.44	0.33	L
Macrobenthos - molluscs	4.49067	2.13435	0.48	1.835E-05	0.00019	62.86944	14	0.4	0.6	16.34605	3.64	29.46	0.13	0.26	L
Macrobenthos - other	72.39182	144.78364	2	0.00019	0.00072	1303.05273	18	0.5	0.5	423.49214	5.85	9	0.34	0.33	L
Megabenthos - filterers	1.31060	4.412	3.37	0.00072	0.12186	13.10599	10	0.3	0.7	2.55567	1.95	2.97	1.73	0.20	L
Megabenthos - other	3.03683	4.03734	1.33	0.03017	0.44889	40.99723	13.5	0.7	0.3	18.65374	6.14	10.15	0.22	0.46	L
Shrimp <i>et al.</i>	0.16948	0.16948	1	0.10362	0.08168	1.52528	9	0.7	0.3	0.69400	4.10	9	0.24	0.46	L
Larval and Juvenile Fish - all	0.25817	3.87258	15	0.01946	2.654E-09	11.61774	45	0.85	0.15	6.41880	24.86	3	0.60	0.55	L
Small Pelagics - commercial	4.54507	1.89210	0.42	2.654E-09	1.00520	9.09014	2	0.85	0.15	5.02230	1.11	4.80	0.38	0.55	L
Small Pelagics - other	1.06021	0.44529	0.42	0.13104	0.00017	2.12043	2	0.65	0.35	0.89588	0.85	4.76	0.50	0.42	L
Small Pelagics - squid	0.13457	0.20185	1.5	0.00016	0.01440	0.37007	2.75	0.85	0.15	0.20446	1.52	1.83	0.99	0.55	L
Small Pelagics - anadromous	0.07724	0.03244	0.42	0.00056	0.02231	0.15449	2	0.85	0.15	0.08536	1.11	4.76	0.38	0.55	L
Medium Pelagics - piscivores & other	0.01131	0.00622	0.55	0.01670	0.01314	0.02306	2.04	0.85	0.15	0.01274	1.13	3.71	0.49	0.55	L
Demersals - benthivores	3.31208	1.49044	0.45	0.00303	0.18545	2.09655	0.63	0.7	0.3	0.95393	0.29	1.41	1.56	0.46	L
Demersals - omnivores	0.30028	0.13513	0.45	0.04298	0.00946	0.24023	0.8	0.65	0.35	0.10150	0.34	1.78	1.33	0.42	L
Demersals - piscivores	6.22812	3.42547	0.55	0.00228	0.39153	7.16234	1.15	0.85	0.15	3.95719	0.64	2.09	0.87	0.55	L
Sharks - pelagics	0.01301	0.00195	0.15	0.09035	0.00031	0.01351	1.04	0.85	0.15	0.00747	0.57	6.92	0.26	0.55	L
Highly Migratory Species	0.01834	0.00917	0.5	0	0.00236	0.07219	3.94	0.85	0.15	0.03989	2.17	7.87	0.23	0.55	L
Pinnipeds	0.09394	0.00633	0.07	7.206E-05	0.00115	0.91121	9.7	0.8	0.2	0.47383	5.04	144.05	0.01	0.52	L
Baleen Whales	0.86075	0.03616	0.04	0.00054	0.00059	3.95944	4.6	0.8	0.2	2.05891	2.39	109.50	0.02	0.52	L
Odontocetes	0.04887	0.00195	0.04	0.00115	0.00014	0.83084	17	0.8	0.2	0.43204	8.84	425	0.00	0.52	L
Sea Birds	0.00588	0.00162	0.275	0.00041	5.878E-05	0.06303	10.72	0.85	0.15	0.03482	5.92	39.00	0.05	0.55	L
Discards	0.44208	0.44208	-	0.00014	-	-	-	-	-	-	-	-	-	-	D
Detritus - POC	81.33333	820.38017	-	5.878E-05	-	-	-	-	-	-	-	-	-	-	D

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